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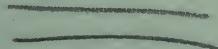
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# EMBRYOLOGICAL AND MORPHOLOGICAL STUDIES ON THE MID-BRAIN AND CERE- BELLUM OF VERTEBRATES

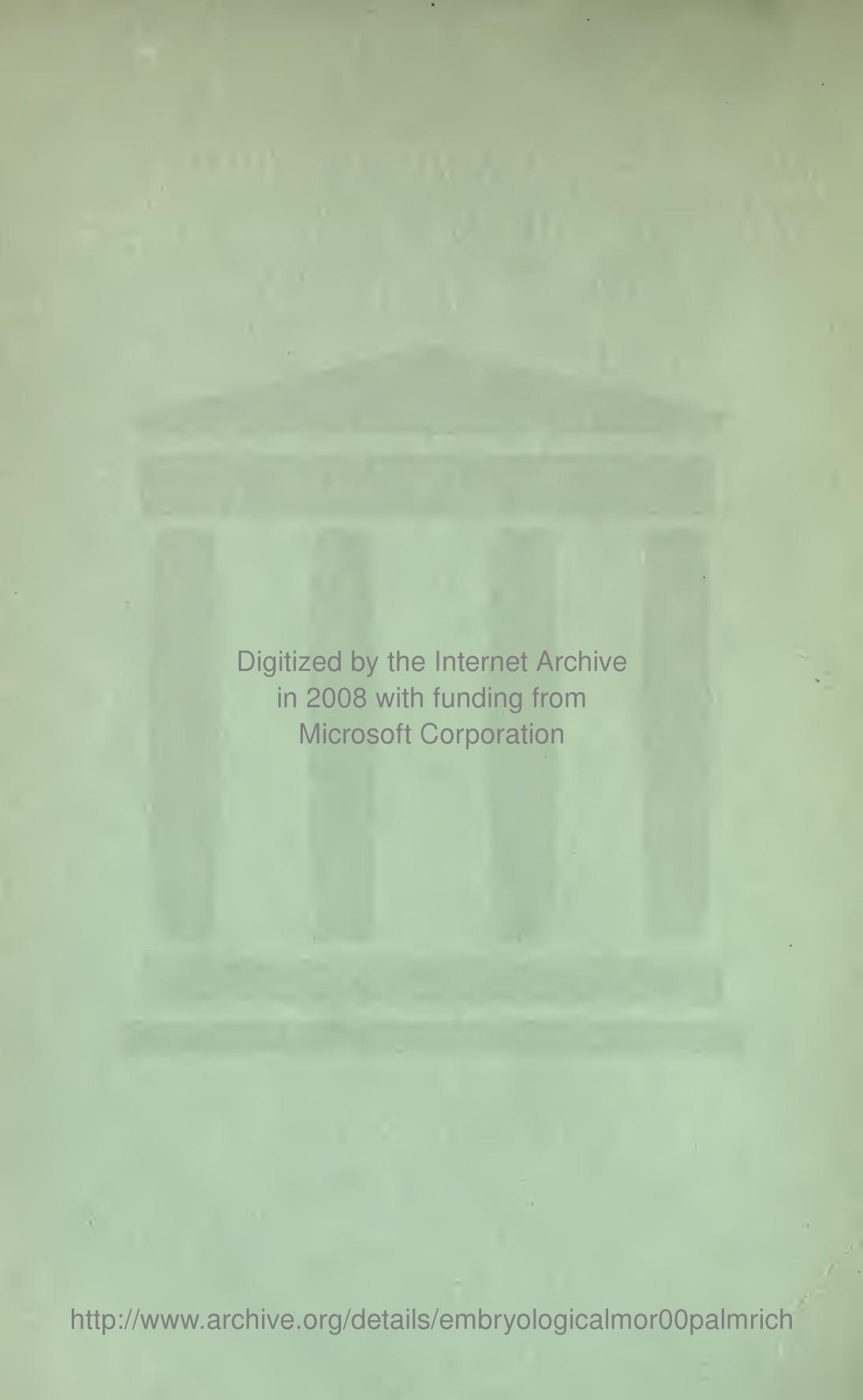
DISSERTATION  
FOR THE DOCTORATE

BY

*AXEL PALMGREN*



STOCKHOLM  
ALB. BONNIERS BOKTRYCKERI  
1921

A very faint, light gray watermark-style illustration of a classical building with four prominent columns supporting an entablature. The building appears to be a temple or a grand hall.

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EMBRYOLOGICAL AND MORPHOLOGICAL  
STUDIES ON THE MID-BRAIN AND CERE-  
BELLUM OF VERTEBRATES

DISSE<sup>T</sup>RAT<sup>I</sup>ON  
FOR THE DOCTORATE  
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BY

*AXEL PALMGREN*  
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STOCKHOLM  
ALB. BONNIERS BOKTRYCKERI  
1921

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# EMBRYOLOGICAL AND MORPHOLOGICAL STUDIES ON THE MID-BRAIN AND CEREBELLUM OF VERTEBRATES

BY

*AXEL PALMGREN.*

With 119 figures in the text.

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## INTRODUCTION.

The embryological development of the vertebrate brain from various points of view has been examined by a great number of authors. Already v. BAER (1837) stated that the brain oriment (in the chick), after the tri-vesicle stage that had previously been described, divides into five vesicles that he named "Vorder-, Zwischen-, Mittel-, Hinter- and Nachhirn". HUXLEY (1871) called these five vesicles: "Prosencephalon (Telencephalon according to the present nomenclature), Thalamencephalon, Mesencephalon, Metencephalon and Myelencephalon". Thanks to GOETTE (1875), MIHALKOWICZ (1877), and other authors our knowledge of the chief characteristics of the morphogeny of the brain was increased.

Undoubtedly His' and KUPFFER's works denote great progress. His' "Zur allgemeinen Morphologie des Gehirns" and KUPFFER's "Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten" and "Die Morphogenie des Centralnervensystems" treats a number of important details in the development of the brain in all vertebrates. In the work last-mentioned KUPFFER has collected and by numerous observations of his own supplemented the results of the morphogenetic investigations in lower vertebrates. Not only His but also GRÖNBERG (1901), ZIEHEN (1905), and others have occupied themselves more especially with researches on the development of the mammalian and human brain.

The much debated question of the segmentation of the head excited interest to study more closely the segmentation of the central nervous system in earlier stages of development. A review of the literature of these questions is given below.

The works treating the embryological development of the nuclei are, on the other hand, relatively few. Just these investigations appear to me to be of the utmost importance.

The preponderant number of conclusions about homology of various nuclei and portions of the vertebrate brain are inferences founded on similar fibre connections of the nuclei. When a nucleus in a lower animal has been proved to have the same or similar connections as a nucleus in a higher animal, the conclusion drawn therefrom was that these nuclei are homologous. Very often little or no regard has been paid to the morphological position of the nuclei, and still less to their ontogenetic formation. In the very idea of homology there is a claim that the homologous portions should be of the same genetic origin. In order to decide if two nuclei, or portions of the brain in two separate types of animals are homologous or not, it is, above all, necessary to investigate, if possible, the embryological origin of these nuclei. If later it can be shown that the nuclei in question have the

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same fibre connections, then a valuable support is naturally given to the conclusion. Fibre connections as decisive factors must be a secondary consideration. In those cases when two brain portions plainly prove to be of the same genetic origin, the nuclei are homologous even if the fibre connections are not precisely the same. The latter are subject to variations in the animal series. Connections existing in a lower animal may be lacking in a higher, while, on the other hand, here new connections may have arisen. The fibre connections of a nucleus may well be comprehended as an expression of its function in one case or the other. But the function of the nuclei has nothing to do with their homology, that being a purely morphological conception.

If, however, it can be proved that two nuclei are formed from the same portion of the neuroblastic layer, thus from the same portion of a (secondary) segment, they are homologous.

Our knowledge of the ontogenetic development, more especially of the mid-brain portions, is as yet very incomplete. Certain portions, as Tectum opticum, Nucleus oculomotorius and Nucleus ruber, have certainly been investigated embryologically, but no more particular and comparative investigation of the formation of the other portions has, so far as I am aware, been undertaken. A comparative investigation of the mid-brain in vertebrates appears to me to be the basis on which the morphology of the mid-brain can be founded. In the following pages I have tried to carry out such an investigation.

These studies have been carried on during the years 1919 and 1920, at the Zootomical Institute of the Stockholms Högskola. Thanks to the extreme kindness of the prefect of the Institute, Professor D:r NILS HOLMGREN, I have been enabled to investigate a portion of the material for research and the abundant collection of neurological preparations belonging to the Institute. For these advantages and the many hints and the interest that Professor HOLMGREN has constantly shown in my investigations I wish to thank him most sincerely.

### MATERIAL AND METHOD.

The examined species and embryological stages are the following:

*Selachii*: *Acanthias vulgaris*, stages of 1,1; 1,4; 1,5; 1,8; 2,0; 2,3; 2,5; 2,7; 3,2; 3,9; 5,0; 5,5; 6,5; 8,0; and 15,0 cm. bodylength measured before the fixation. Fixation in Carnoys fluid. Stain: haemalum according to Mayer or Cresyl violet.

*Ganoidei*: 1) *Acipenser ruthenus*, adult. Fixation in alkohol. Stain: iron haematoxylin according to Heidenhain. One series of transverse sections.

2) *Lepidosteus osseus*, of 13,0 cm. bodylength. Fixation in alkohol. Stain: Cresyl violet. Two series of transverse sections.

**T**eleostii: 1) *Salmo salvelinus*, stages of 0,6; 0,7; 0,8; 0,9; 1,0; 1,1; 1,2 cm. bodylength and of 1 (A), 3 (B), 10 (C), 46 (D) and 64 (E) days after hatching. Fixation in Bouins fluid. Stain: haemalum according to Mayer.

2) Adult brains of *Salmo salvelinus*, *Osmerus eperlanus*, *Labrus rupestris* and others.

**A**mphibia: *Rana temporaria*, stages of 0,4; 0,5; 0,6; 0,7; 0,8; 1,0; 1,5; 2,0; 3,0; 3,6 cm. bodylength and newly metamorphosed young and adult frogs. Fixation in Bouins fluid. Stain: haemalum according to Mayer.

**R**eptilia: *Tropidonotus natrix*, a stage with four body spirals. Fixation in alkohol. Stain: haemalum.

**A**ves: *Gallus domesticus*, stages of 50, 60 hours and 4, 4½, 5, 6, 7, 8, 8½, 9, 10, 15, 19 days of incubation. Fixation in Bouins fluid. Stain: haemalum according to Mayer or Cresyl violet.

**M**ammalia: *Mus musculus* var. *albino*, stages of 0,5; 0,55; 0,6; 0,7; 0,8; 1,0; 1,3; 1,6; 1,9; 2,3; 4,0; 4,5 cm. bodylength and adult specimens. Fixation in Bouins fluid. Stain: haemalum according to Mayer or Cresyl violet.

## I. THE MESENCEPHALON.

In order to have fixed points from which to determine e. g. the morphological position of a nucleus, I have tried as accurately as possible, to draw the boundary-lines between the Mesencephalon and adjacent parts of the brain and then subdivided the Mesencephalon into fixed smaller portions. The anterior and posterior boundary-planes of the mid-brain have been determined in conformity with the boundary-planes of the Encephalomeres or segments<sup>1</sup>, in the same manner to be found in all vertebrates. These segments are indeed, distinct as such, i. e. as dilatations separated by external constrictions, and internal ridges, only in comparatively early embryonic stages. I think, nevertheless, that I have succeeded in following their original boundaries to later stages, and in determining these boundaries in relation to differentiated structures. A transversal division of the Mesencephalon has thereby been obtained.

A longitudinal division has been obtained partly guided by ventricular sulci, partly also by the cell-formation itself.

I begin by describing the development of the mesencephalic segments.

<sup>1</sup> By segments is meant in the following, the so-called secondary segments. The question of the importance of these segments, from the point of view of the segmentation of the head, lies outside the scope of this investigation.

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### I. THE MESENCEPHALIC SEGMENTS.

McCLURE (1889) and KUPFFER (1885, 1893) were the first to state that the segmentation of the Met- and Myelencephalon, earlier described, extends forward to the anterior part of the brain. The number of segments in front of Fissura rhombo-mesencephalica have, by ZIMMERMANN (1891), FRORIEP (1892), WATERS (1892), KUPFFER (1893), LOCY (1894, 95), NEAL (1898), HILL (1899) and others, been fixed at five. ZIMMERMANN, NEAL, FRORIEP and KUPFFER (1893) assigned three segments to the Mesencephalon, namely, segments 3, 4 and 5; WATERS, McCLURE, HILL and KUPFFER (1905) two segments (4 and 5). The Mesencephalon was previously considered by, e. g. ORR (1887), and others, to be formed of only one segment.

I agree with this last-named investigator in so far as that the Mesencephalon is formed by the fourth segment, while, in all the animal types I have examined, the fifth segment is completely reduced. At early embryonic stages however, two segments, the fourth and fifth, must be assigned to the mid-brain.

The third segment has by KUPFFER been termed Synencephalon and by him been assigned to the 'tween-brain (Diencephalon) together with the second segment or Parencephalon.

The earlier assignment of the third segment to Mesencephalon was on the following grounds: as KUPFFER, NEAL and others stated, it is possible at certain embryonic stages of all vertebrates, to distinguish two folds on the ventral side of the brain, the posterior one is the Plica encephali ventralis; the anterior one is a fold which bounds the hypothalamic region caudad. This latter fold continues as a groove, Fissura proso-mesencephalica, round the brain, and divides an anterior part, Prosencephalon, from a posterior, Mesencephalon of HUXLEY. This posterior part is later subdivided into three segments.

NEAL (1898) has however, stated that the Commissura posterior develops between segments 3 and 4. At the dorsal anterior edge of the third segment, the Epiphysis is formed. Nervus III starts from segment 4.

Thus the boundary-line Commissura posterior-Tuberculum posterius (His) (or behind Tuberculum posterius [KUPFFER]) does not coincide with the segmental groove between Pros- and Mesencephalon in earlier stages. I believe it to be most suitable, on grounds which I give later, to draw the boundary between the 'tween-brain and the mid-brain, between segments 3 and 4, and thus in accordance with KUPFFER (1905), assign segment 3 (Synencephalon) to the 'tween-brain (Diencephalon). To the Mesencephalon I thus assign segments 4 and 5.

A. Selachii (*Acanthias vulgaris*).

In parasagittal sections of the brain of an embryo of *Acanthias* at stage 1,1 cm., it is easy to distinguish the segments (Fig. 1). (Compare KUPFFER [1905], Fig. 89). Of the five segmental dilatations, which lie before the Fissura rhombo-mesencephalica, the first forms, as is known, the Telencephalon the second and third respectively Parencephalon and Synencephalon, and the last two, Mesencephalon. As long as the segments are distinct, they are separated from each other, partly by grooves or constrictions, partly by inner ridges, corresponding with these grooves. Between the grooves the segments protrude somewhat outwards (ORR [1887]). The boundary-grooves as well as the ridges at stage 1,1 cm. are only developed on the lateral walls of the brain, and thus do not appear on the medial sagital sections. This does not however apply to Fissura rhombo-mesencephalica, which is a circular fissure or nearly so. So far as I know, it has not hitherto been possible to observe the two mesencephalic segments of *Acanthias* in later stages of development; the Mesencephalon is said to become unified very soon.

At stage 1,5 cm. it is still possible to observe the segments in the same manner as in stage 1,1 cm. An important change has, however, taken place. While at stage 1,1 cm. the two mesencephalic segments are approximately of the same size, at stage 1,5 cm. the anterior segment is considerably larger than the posterior (Fig. 2).

On Fig. 3, which represents a more medial section of the same series as that shewn in Fig. 2 the boundary-ridge between the Synencephalon and the first mesencephalic segment (boundary-ridge S—M<sub>1</sub>) is touched, the boundary-ridge M<sub>1</sub>—M<sub>2</sub> is intersected.

A section in the direction given by the line 4—4 Fig. 3, is given in Fig. 4. The considerably larger M<sub>1</sub>-segment is here separated from the M<sub>2</sub>-segment by a small depression in the lateral walls of the brain, boundary-groove M<sub>1</sub>—M<sub>2</sub>. Fissura rhombo-mesencephalica also appears distinctly.

A comparative study of stages 1,5, 1,8 and 2,0 cm. gives the answer to the question as to what becomes of the segment M<sub>2</sub>. A parasagittal

Fig. 1. Parasagittal section of *Acanthias* at stage 1,1 cm. Figs. 2, 3. Parasagittal sections of *Acanthias* at stage 1,5 cm. Fig. 4. Horizontal section of *Acanthias* at stage 1,5 cm. Fig. 5. Parasagittal section of *Acanthias* at stage 2,0 cm. Fig. 6. Horizontal section of *Acanthias* at stage 2,0 cm. (Microphotographs.)

C, Cerebellum; F. m<sub>1</sub>—m<sub>2</sub>, the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; M<sub>1</sub>, the anterior mesencephalic segment; M<sub>2</sub>, the posterior mesencephalic segment; N. III, Nervus oculomotorius; P, Parencephalon; r. m<sub>1</sub>—m<sub>2</sub>, the boundary-ridge between the mesencephalic segments; r. s—m<sub>1</sub>, the boundary-ridge between the Syn- and Mesencephalon. S, Synencephalon; T, Telencephalon.

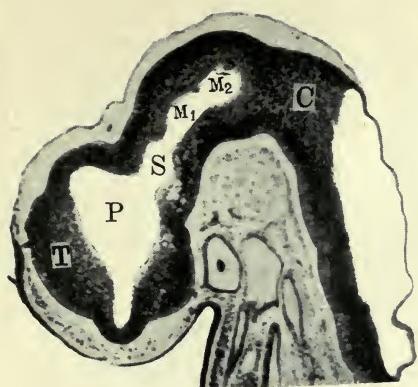


Fig. 1.

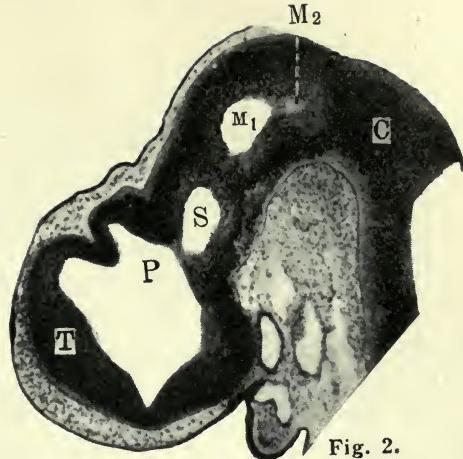


Fig. 2.

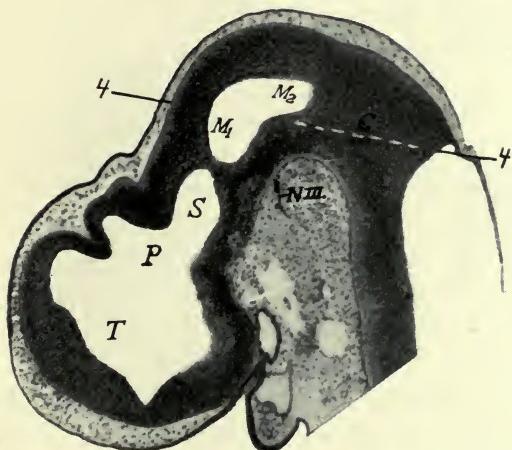


Fig. 3.

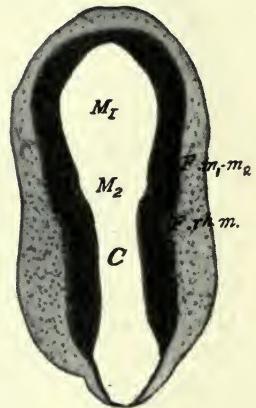


Fig. 4.

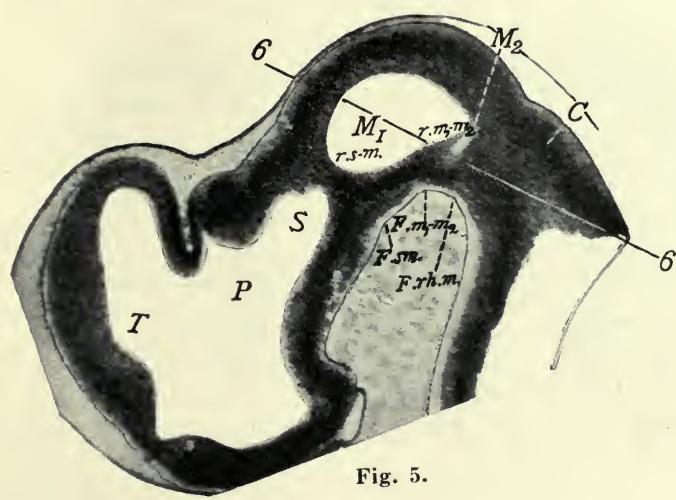


Fig. 5.

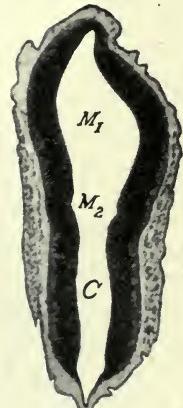


Fig. 6.

section of stage 2,0 cm. shews the now immense difference in size between the  $M_1$ - and the  $M_2$ -segments (Fig. 5). The boundary-ridge  $S-M_1$  and likewise the ridge  $M_1-M_2$  are touched. It is now easy by means of a horizontal section in the direction given by the line 6—6, to prove that the  $M_2$ -segment has been reduced, or as it appears, compressed by the growth of the  $M_1$ -segment, so that a groove has been formed. This groove is Sulcus intraencephalicus posterior of KUPFFER (Fig. 6).

A distinct impression of the compression of the  $M_2$ -segment during the process of development is given by the features received from sections of a somewhat later stage (2,7 cm.) (Fig. 7).

On the parasagittal section, Fig. 7, structural features corresponding to those in Fig. 5 of the 2,0 cm. stage are shewn. Sulcus intraencephalicus posterior has become considerably deeper and more sharply defined, which is best seen on horizontal sections in the direction given by the line 8—8 Fig. 7 (Figs. 8 and 9). At stages 1,8 to 3,2 cm. in *Acanthias*, Sulcus intraencephalicus can be traced from the region of the Velum anticum downwards along the inner side of the lateral walls. There is no dorsal or ventral connection between the two laterally developed sulci. In other words, Sulcus intraencephalicus posterior is not visible on the medial sagittal section.

In further support of my view on the connection between the  $M_2$ -segment and Sulcus intraencephalicus posterior, it may be stated that the posterior oculomotor fibres, which, like the whole Nervus III, emerge from the brain between the ridges  $S-M_1$  and  $M_1-M_2$  (Fig. 3, compare also NEAL [1898]) at the same time as the vigorous development of the  $M_1$ -segment and the compression of the  $M_2$ -segment, will lie nearer to Fissura rhombo-mesencephalica, without however, passing the boundary between the  $M_1$ - and  $M_2$ -segments.

In order to prove that Sulcus intraencephalicus posterior is the inner concavity of the reduced  $M_2$ -segment, it may be asserted: 1) At stages 1,5—2,7 cm. a reduction in the size of the  $M_2$ -segment can be traced step by step; 2) The boundary-ridges  $M_1-M_2$  are displaced more and more caudad, and limit the Sulcus intraencephalicus posterior frontad; 3) Nervus oculomotorius, which, at stage 1,5 cm., lies comparatively far in front of

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Fig. 7. Parasagittal section of *Acanthias* at stage 2,7 cm. Fig. 8. Horizontal section of *Acanthias* at stage 2,7 cm. Fig. 9. Detail of the section Fig. 8 showing the Sulcus intraencephalicus. Fig. 10. Sagittal section of *Acanthias* at stage 2,0 cm. Figs. 11 and 12. Sagittal and parasagittal sections through the ventro-medial part of the mid- and hind-brain of *Acanthias* at stage 2,7 cm. (Microphotographs.)

C, Cerebellum; E. i., Eminentia interpeduncularis; F. i., Fovea isthmi; F.  $m_1-m_2$ , the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; M., Mesencephalon;  $M_1$ , the anterior mesencephalic segment; P., Parencephalon; S., Synencephalon; S. i. p., Sulcus intraencephalicus posterior; T., Telencephalon.

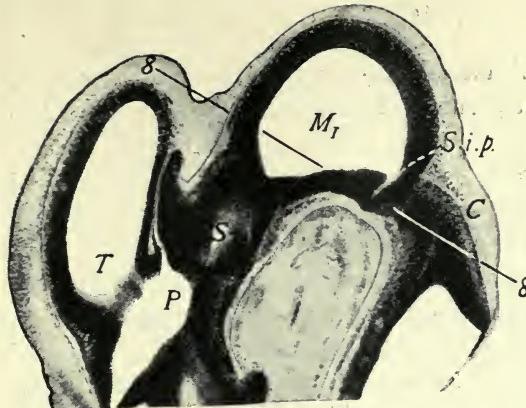


Fig. 7.

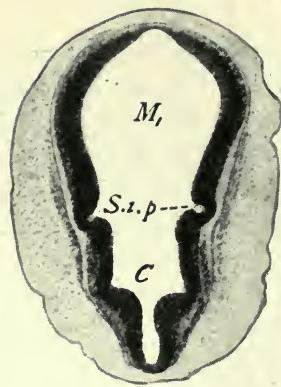


Fig. 8.

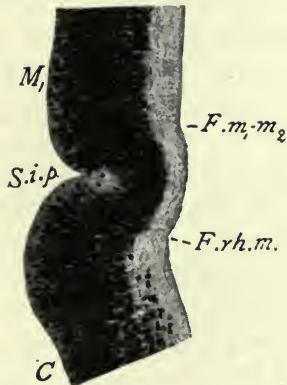


Fig. 9.

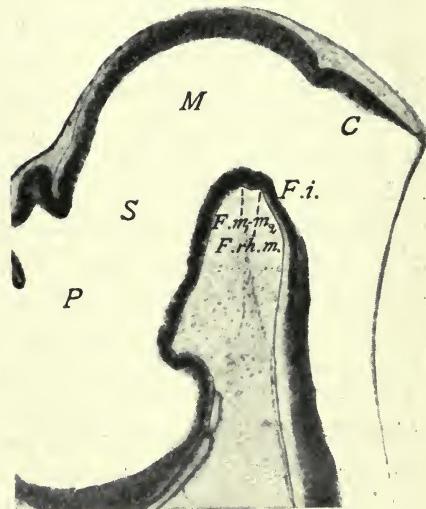


Fig. 10.

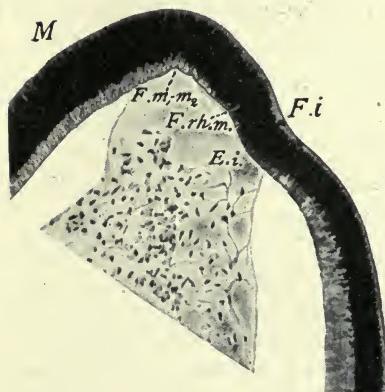


Fig. 11.

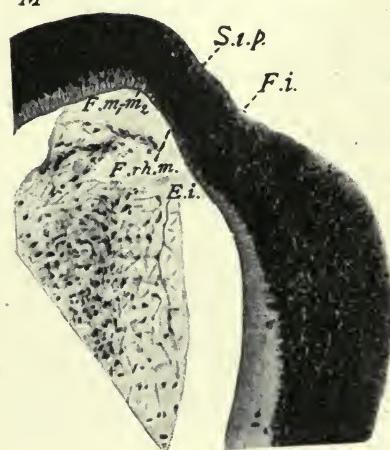


Fig. 12.

Fissura rhombo-mesencephalica within the  $M_1$ -segment, is displaced caudad (while retaining its morphological position) in the same degree as the  $M_2$ -segment becomes reduced.

By Sulcus intraencephalicus posterior, then I mean the groove, described by KUPFFER and others, which in certain embryonic stages recurs in the whole of the vertebrates in the inner side of the lateral walls of the brain between the Mes- and Metencephalon or more correctly in the caudal part of the Mesencephalon. These grooves are not, as will directly be shewn, connected with the Fovea isthmi of HERRICK ("hintere Mittelhirngrenze" of BURCKHARDT, "Isthmusgrube" of HIS, Sulcus interencephalicus of HALLER), which are sometimes, in works bearing on the subject (by KUPFFER, amongst others), named Sulcus intraencephalicus and described as the ventral part of the lateral Sulci intraencephalici.

In order to prove this more clearly, it is necessary first to determine the position of the Fissura rhombo-mesencephalica in relation to Sulcus intraencephalicus and Fovea isthmi. As already stated, this is the most distinct of the boundary-grooves. At the earlier stages (1,1 cm.) the groove is about equally well-defined all round the brain. Later (stage 1,5 cm. etc.) it becomes laterally more obsolete, while ventrally and dorsally it appears continually more distinct and clearly defined. At stage 2,0 cm. (Fig. 10) Fissura rhombo-mesencephalica<sup>1</sup> lies immediately in front of the depression in the floor of the brain, called by HERRICK Fovea isthmi.

In front of Fissura rhombo-mesencephalica appears at stage 2,0 cm. (Fig. 10) another fairly distinct groove with about the same lateral extension as this fissure. This just-mentioned groove lies opposite the boundary-ridge  $M_1—M_2$ , and can therefore be described as the boundary-groove between the  $M_1$ - and  $M_2$ -segments (F.  $m_1—m_2$  Fig. 10, comp. also NEAL [1898]).

The boundary-groove  $M_1—M_2$  becomes later continually clearer and more distinct (stage 2,7 cm. Fig. 11) and then forms the apex of the cranial flexure. Somewhat behind this, Fissura rhombo-mesencephalica is to be found. (F. rh. m. Fig. 11)<sup>2</sup>. Thus Fovea isthmi clearly lies behind Fissura rhombo-mesencephalica, that is, to say, in the cerebellar neuromere, while Sulcus intraencephalicus lies in front of Fissura rhombo-mesencephalica (comp. KUPFFER [1905]).

A longitudinal section immediately lateral to the medial plane of stage 2,7 cm. (Fig. 12) is especially illuminating. Between the boundary-groove

<sup>1</sup> In spite of the groove having already become considerably indistinct laterally, it can yet be maintained with certainty, that the groove marked F. rh. m. in Fig. 10 is Fissura rhombo-mesencephalica. In the series of sagittal sections of the stage 1,5 cm., it can namely be traced as a distinct groove, at least far enough in a lateral direction to prove that it corresponds to the boundary-ridge between the Mes- and Metencephalon.

<sup>2</sup> It is to be noticed that both at stage 2,0 and 2,7 cm. Fissura rhombo-mesencephalica lies immediately in front of Fovea isthmi, and is thus the same in both cases.

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$M_1-M_2$  (F.  $m_1-m_2$  Fig. 12) and Fissura rhombo-mesencephalica (F. rh. m. Fig. 12) lies Sulcus intraencephalicus posterior (S. i. p. Fig. 12) and a little behind this a groove (F. i. Fig. 12) issuing from Fovea isthmi (comp. below). By following the series of sections it is easy to prove that this interpretation of the grooves is the correct one. It is not possible to point out the slightest connection between them.

Sulcus intraencephalicus posterior, which in stages 2,7 to 3,2 cm. is a deep groove, does not remain as such in later stages. This is, on the contrary the case with Fovea isthmi, which is to be found, as we know, in the adult brain. Sulcus intraencephalicus posterior however, does fortunately not disappear without leaving traces. While still at its clearest (stage 2,7 cm.) it is already surrounded by a relatively cell-free substance<sup>1</sup>, which can be found again in later stages (Fig. 9).

At stages 5,0 to 8,0 cm., when the ependymal-layer has been differentiated, a distinct ependymal-thickening has been formed, which surrounds the above-mentioned cell-free substance (r. S. i. p. Fig. 13). Of this ependymal-thickening is later formed (stage 15,0 cm.) a layer of closely-packed, typical ependymal cells, which lies under an inner layer with only a few of such cells (r. S. i. p. Fig. 14). This latter layer, deficient of cells, has been formed from the above-mentioned relatively cell-free substance. In consequence of this peculiar arrangement of cells, it is possible even in the fully developed brain, to ascertain the exact position of the rudiment of Sulcus intraencephalicus posterior. The ependymal-strand, which lies under the rest of the ependymal-layer, can easily be traced from the region of the Velum anticum down to the "Haubenwulst" of His, thus in the same position and extension as Sulcus intraencephalicus posterior.

From the anterior part of Fovea isthmi issues a groove (comp. stage 2,7 cm. Fig. 12) which, at stage 15,0 cm., becomes extraordinarily distinct (F. i. Fig. 15). This groove does not extend further than to the inner side of the "Haubenwulst", and is thus a transverse groove in Sulcus longitudinalis ventralis. Fovea isthmi itself, becomes (stages 6,5 to 15,0 cm.) more and more compressed so as to form the ventral part of the transverse groove just-mentioned.

Simultaneously with the disappearance of Sulcus intraencephalicus, the distance between Fissura rhombo-mesencephalica and the boundary-groove  $M_1-M_2$  is shortened; these grooves, as already mentioned, appear on the ventral side of the brain at stages 2,0 to 2,7 cm. (Figs. 10, 11). Already at stage 3,2 cm. (Fig. 16) these grooves lie nearer each other than at stage 2,7 cm. and at last at stages 3,9 to 5,5 cm. (Fig. 17) they lie so close

<sup>1</sup> Comp. ORR's (1887) definition of neuromeres: "The nuclei are generally nearer the outer surface, and approach the inner surface only toward the apex of the ridge" (p. 335).

together, that one can hardly speak of them as separate grooves. The unified groove or depression thus formed HIS (1892, a) names the Fossa interpeduncularis. As it however clearly lies within the boundary-plane, I continue to call it Fissura rhombo-mesencephalica.

Taking also into consideration, that only very few cells are formed from the neuroblastic layer of the  $M_2$ -segment it should be rightly asserted that little more than a lamel of the  $M_2$ -segment remains between the Mes- and Metencephalon at the later stages and in the adult brain. The rudiment of the  $M_2$ -segment, which really lies immediately anterior to the boundary between the Mes- and Metencephalon, can practically be said to form a boundary-plane between these parts of the brain in the later stages of development.

### B. Teleostii (*Salmo salvelinus*).

According to WATERS (1892), the mid-brain of Teleosts (*Gadus*) contains two segments.

According to HILL (1899), who has likewise found two segments in the Mesencephalon of *Salmo*, these segments are bounded by outer and inner grooves, instead of inner ridges, as for the most part, at least in later stages, in the other types of animals.

HILLS, Figs. 12—15, Taf. 28, and Textfigure D. (page 410), of *Salmo* at the stages of 24—32 days' incubation, seem to agree with my Fig. 18, which represents a parasagittal section of the brain of an embryo of *Salmo salvelinus* at stage 0,6 cm. The inner groove (S. i. p. Fig. 18), which, according to HILL, bounds the posterior mid-brain segment caudad, is in this case, Sulcus intraencephalicus posterior.

This groove, as well as that described by HILL, as the boundary-groove between the mid-brain segments, lies clearly, at least at stage 0,6 cm., intra-segmentally and not intersegmentally. I have not had the opportunity of investigating what the case is in earlier stages. As a distinct Sulcus intraence-

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Figs. 13 and 14. Details of transverse-sections of *Acanthias* at stages 5,0 and 15,0 cm. Fig. 15. Horizontal section through the Sulcus longitudinalis ventralis in *Acanthias* at stage 15,0 cm. Figs. 16 and 17. Sagital sections through the ventro-medial part of the mid- and hind-brain of *Acanthias* at stages 3,2 and 5,5 cm. Fig. 18. Parasagittal section of *Salmo* at stage 0,6 cm. Fig. 19. Sagital section of *Salmo* at stage 0,6 cm. (Microphotographs.)

C, Cerebellum; E. i., Eminentia interpeduncularis; F. i., Fovea isthmi; F.  $m_1$ - $m_2$ , the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; H, the hypothalamic region; M, Mesencephalon; Nc. IV, Nucleus trochlearis; P, Parencephalon; r. S. i. p., the rudiment of the Sulcus intraencephalicus posterior; S, Synencephalon; S. i. p., Sulcus intraencephalicus posterior; S. l. v., Sulcus longitudinalis ventralis; T, Telencephalon.



Fig. 13.



Fig. 14.

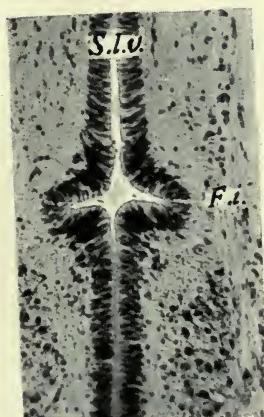


Fig. 15.

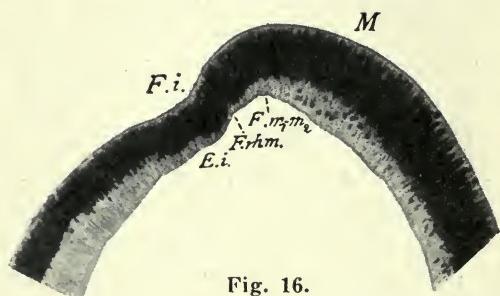


Fig. 16.

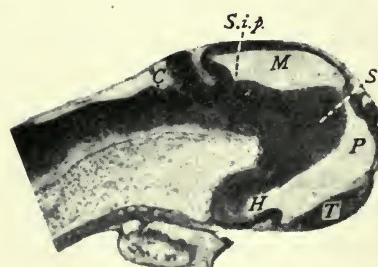


Fig. 18.

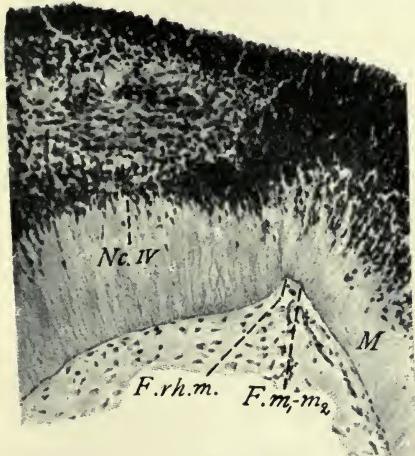


Fig. 17.

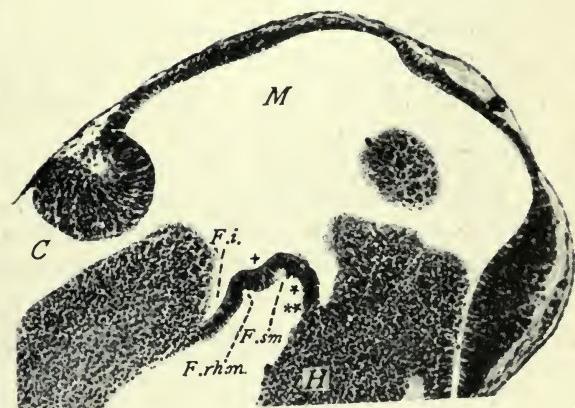


Fig. 19.

phalicus exists at certain stages of *Salmo*, it may readily be assumed that this groove has arisen in like manner in the Teleosts, as e. g. in *Acanthias*. What however is of greater importance for this investigation, is that *Salmo* at 0,6 cm. and older stages is in conformity with the other animal-types at corresponding stages.

At the earliest stages (0,6 and 0,8 cm.) available to me for investigation, Sulcus intraencephalicus is thus already fully developed. In the lateral sections of a series of sagital sections of stage 0,6 cm., the mesencephalic ventricle has the form of a triangle, whose ventral apex is constituted by Sulcus intraencephalicus. This groove can be followed section by section down towards Sulcus longitudinalis ventralis. In the medial plane in front of Fissura rhombo-mesencephalica there is indeed to be found a depression in the floor of the mid-brain (+ Fig. 19) (comp. KUPFFER [1905] Fig. 148), but this is limited towards the front by a groove, which later will be shewn to be the boundary-groove between the Syn- and Mesencephalon, and thus to be Fissura syn-mesencephalica. This groove must therefore not be compared with the boundary-groove  $M_1 - M_2$ , which in *Acanthias* bounds Sulcus intraencephalicus frontad. The medial depression is thus not the ventral part of Sulcus intraencephalicus, as KUPFFER asserts. The boundary-groove  $M_1 - M_2$  does not occur in *Salmo* at the stages which I have had available for investigation. It may possibly be found at earlier stages.

Immediately behind Sulcus intraencephalicus (S. i. p. Fig. 20), which distinctly lies in front of the Fissura rhombo-mesencephalica, lies another similar groove (F. i. Fig. 20) in the same position and with the same extension as that which issues from Fovea isthmi in *Acanthias* (F. i. Fig. 12). An insignificant ridge divides these grooves: the boundary-ridge  $M_2 - Mt$ . (r.  $m_2 - mt$ . Fig. 20). Fovea isthmi, like the lateral groove emerging from it, lies immediately behind Fissura rhombo-mesencephalica. Neither can I, in *Salmo*, discover any connection between these grooves.

In all these respects, *Salmo* is in accord with *Acanthias*.

By reason of the ventro-lateral parts of the mid-brain in *Salmo* not being vertically raised as in *Acanthias* embryos, but lying more or less horizontally (comp. Figs. 57 and 71), Sulcus intraencephalicus posterior describes a curve, from Sulcus longitudinalis ventralis upwards. (In consequence of this, the dorsal parts of Sulcus intraencephalicus are not visible on horizontal sections as in *Acanthias*).

As late as stage 0,9 cm. there is no trace of a ventral communication between the lateral Sulci intraencephalici. Such a communication is, however, found later. The cause of this seems to be, that the boundary-ridge  $M_2 - Mt$ . becomes ventrally considerably higher than at earlier stages, while at the same time the ventro-medial part of the mid-brain thickens. At stage 1,0 cm. two distinct ventral grooves have thus been formed (Fig. 21) (comp.

## STUDIES ON THE MID-BRAIN AND CEREBELLUM

KUPFFER's [1905] Fig. 150). The anterior groove is Sulcus intraencephalicus (S. i. p. Fig. 21), the posterior is Fovea isthmi (F. i. Fig. 21) (not Sulcus intraencephalicus as KUPFFER affirms), which, in *Salmo* also has been compressed to a well-defined groove.

Step by step, in the stages up to 1,2 cm. a fusion of these grooves can be observed, that is to say the boundary-ridge  $M_2$ —Mt. (r.  $m_2$ —mt. Fig. 21) disappear more and more. In this way is formed the large and well-defined medial groove or depression, which, in the fully developed brains of e. g. *Salmo*, *Osmerus*, *Labrus* and others, lies on the floor of the brain under the Valvula cerebelli (F. i. Fig. 52). It is thus established that in *Salmo* there is a fusion between Fovea isthmi, which lies behind the boundary-plane between the Mes- and Metencephalon, and Sulcus intraencephalicus, which lies in front of the same. This entitles us all the more, at later stages, to use the rudiments of the posterior Mesencephalon segment as boundary-marks. The lateral parts of Sulcus intraencephalicus disappear completely a few days after hatching. (Regarding the remaining traces of it and the boundary-zone, see page 16).

### C. Amphibia (*Rana temporaria*).

The segmentation of the amphibian brain has been examined by WATERS (1892) (*Amblystoma*), McCLURE (1889) (*Amblystoma*), KUPFFER (1885, 1905) (*Salamandra*) and others. The number of segments in front of Fissura rhombo-mesencephalica is five, two of which belong to the mid-brain.

The stage 0,4 cm. of *Rana* can be said to correspond with stage 1,5 cm. of *Acanthias*, in so far as that, in the former, the anterior Mesencephalon segment is distinctly larger than the posterior. The segments are mostly clearly defined on horizontal sections (Fig. 22). The protrusion of the posterior segment, forms, in *Rana*, Sulcus intraencephalicus posterior, which, even at only slightly later stages (0,5 cm.) becomes characteristically developed as a well-defined groove, after which it increases in distinctness and depth. Towards the dorsal side it can be traced in the same way as in *Gallus* (see page 20). At the stages of about 3 cm. body-length, Sulcus intraencephalicus commences growing together, and by, e. g., stage 3,6 cm., becomes almost defaced.

Already at stage 0,7 cm., the floor of the groove is formed of cells, which, by reason of their bi-polar shape and greater receptibility to stains, are distinguishable from the neighbouring cells. At later stages these cells remain in the form of an ependymal-thickening on the point where Sulcus intraencephalicus was situated. From these cells issue thick ependymal-fibres towards the surface of the brain (e. f. Fig. 23). Owing to the fact that

Sulcus intraencephalicus in comparatively late stages, lies near or in the boundary-plane  $M_2$ —Mt. itself, this ependymal line must be considered as a boundary-zone (z. Fig. 24). A similar boundary-zone is also to be found in *Salmo* at stages 0,9 cm. — D. (z. Fig. 119).

In none of the stages, which I have examined, Sulcus intraencephalicus has been ventro-medially developed; it is, however, possible, e. g. at stage 3,0 cm., to trace Sulcus intraencephalicus to sections which lie immediately beside the medial plane, where a very well-defined Fissura rhombo-mesencephalica is ventrally developed. This groove clearly lies behind Sulcus intraencephalicus. On the medial section a rather indistinct ventral eminence (the boundary-ridge  $M_2$ —Mt. [r.  $m_2$ —mt. Fig. 25]) is perceptible which lies opposite to Fissura rhombo-mesencephalica (F. rh. m. Fig. 25). At stage 3,6 cm. this eminence is to be found in the same position as in stage 3,0 cm. (r.  $m_2$ —mt. Fig. 26). Caudally to this, the floor part of the Metencephalon is somewhat concave. This concavity, Fovea isthmi (F. i. Figs. 25, 26) develops more and more in later stages, and remains in the fully developed brain as a well-defined depression in the Isthmus region.

#### D. Reptilia:

In regard to reptiles, I have had access only to a series of sagittal sections of *Tropidonotus natrix* (at the stage with 4 body-spirals) and some older stages of *Iguana* sp. This lack of material is so much the more to be deplored, as it is exactly in *Tropidonotus*, (the  $2\frac{1}{2}$  body-spiral stage) that KUPFFER (1905) described and figured a larger posterior and a lesser anterior Mesencephalon segment (see Fig. 245 of KUPFFER). The posterior segment would thus in *Tropidonotus* form the greater part of the mid-brain, the  $M_1$ -segment being reduced.

It is clear that such an interpretation of the figured structural features

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Fig. 20. Parasagittal section of *Salmo* at stage 0,6 cm. Fig. 21. Sagittal section through the ventral part of the mid-brain in *Salmo* at stage 1,0 cm. Fig. 22. Horizontal section of *Rana* at stage 0,4 cm. Fig. 23. Detail of an horizontal section of *Rana* at stage 2,0 cm. Fig. 24. Parasagittal section of *Rana* at stage 3,6 cm. Fig. 25. The ventro-medial part of the mid-brain in *Rana* at stage 3,0 cm. (Microphotographs.)

C, Cerebellum; D. IV, the decussation of Nervus IV; e. f., ependymal fibres; F. i., Fovea isthmi; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura synmesencephalica; H, the hypothalamic region; I, the infundibular region; M, Mesencephalon;  $M_1$  and  $M_2$ , the two mesencephalic segments; M. o., Medulla oblongata; r.  $m_2$ -mt, the boundary-ridge between the Mes- and Metencephalon, R. p. m., Recessus posterior mesencephali, S. i. p., Sulcus intraencephalicus posterior; T. p., Tuberculum posterius; T. s., Torus semicircularis; Z-Z, the boundary-zone between the Mes- and Metencephalon; v, the vacuolization in the Tuberculum posterius; Vl. c., Valvula cerebelli.

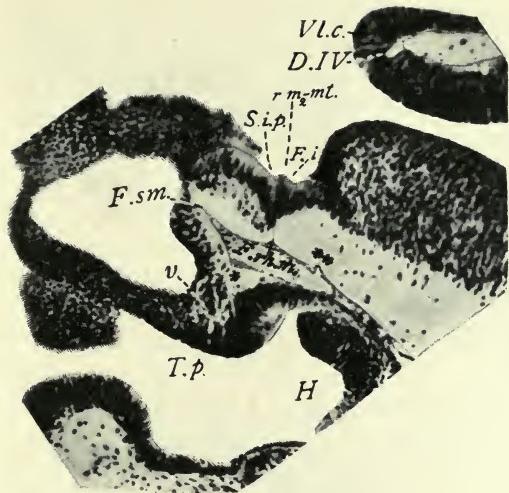


Fig. 21.

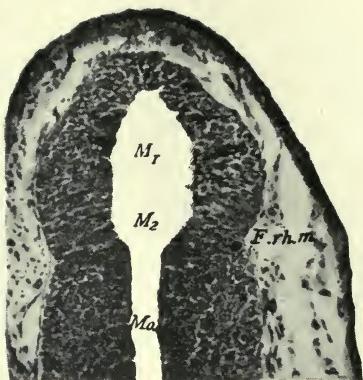


Fig. 22.

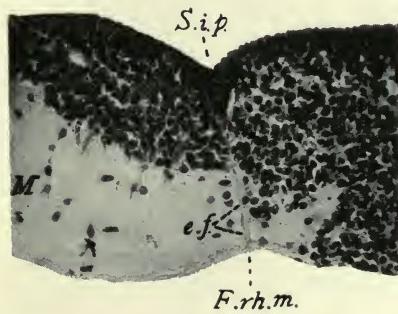


Fig. 23.

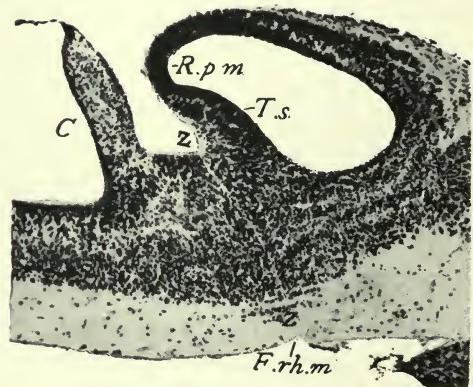


Fig. 24.

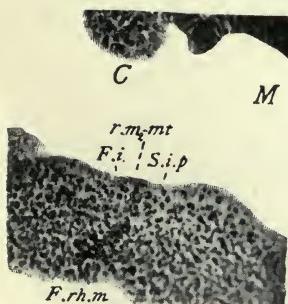


Fig. 20.

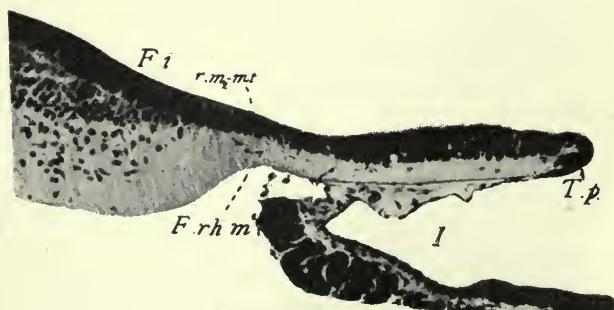


Fig. 25.

of *Tropidonotus* postulate a different course of development of the mesencephalic segments, than that above described. At the stage examined by me, which is considerably older than that described by KUPFFER, I have been unable to find any trace of a lesser anterior Mesencephalon-segment. KUPFFER (1893) states that these mesencephalic segments occur in like manner in Birds (ducks). If this is the case, I think I can give an explanation of the so-called "anterior" Mesencephalon-segment in *Tropidonotus* (see below page 22).

#### E. Aves (*Gallus domesticus*).

Figs. 27, 28, of *Gallus domesticus* at stages of 50 and 60 hours of incubation, represent parasagittal sections through the point where Nervus III emerges from the brain. At the stage of 50 hours, the oculomotor nerve (N. III Fig. 27) lies comparatively far in front of Fissura rhombo-mesencephalica (F. rh. m. Fig. 27) and immediately in front of a groove which, by comparing with *Acanthias* at the 1,5 and 2 cm. stages, may be defined as the boundary-groove M<sub>1</sub>—M<sub>2</sub> (F. m<sub>1</sub>—m<sub>2</sub> Fig. 27). A gradual displacement of Nervus III caudad towards Fissura rhombo-mesencephalica can be clearly established (comp. TANDLER AND KANTOR [1907]), i. e. the region between the groove M<sub>1</sub>—M<sub>2</sub> and the Fissura rhombo-mesencephalica (the M<sub>2</sub>-segment) is clearly reduced<sup>1</sup>.

At the stage of 60 hours a well-defined posterior segment can be observed in the horizontal section (M<sub>2</sub> Fig. 29), corresponding to that of *Acanthias* at stage 1,5 cm. figured in Fig. 4. It is obvious that in a parasagittal section of this stage, a structural feature approximately corresponding to Fig. 2 (stage 1,5 cm.) of *Acanthias* would be received if the line a—a Fig. 29 were parallel with the longitudinal axis, i. e. the direction of the section.

<sup>1</sup> It should be observed, that the Nervus III the whole time behelds the same position to the cell-structure. The displacement cannot thus be explained by new fibres having formed behind those already existing.

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Fig. 26. The ventro-medial part of the mid-brain of *Rana* at stage 3,6 cm. Fig. 27. Parasagittal section of *Gallus* at stage 50 hours. Fig. 28. Parasagittal section of *Gallus* at stage 60 hours. Fig. 29. Horizontal section of *Gallus* at stage 60 hours. Fig. 30. Sagittal section of *Gallus* at stage 50 hours. Fig. 31. Sagittal section of *Acanthias* at stage 1,8 cm. (Microphotographs.)

C, Cerebellum; F. i., Fovea isthmi; F. m<sub>1</sub>—m<sub>2</sub>, the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; I, the infundibular region; M, Mesencephalon; M<sub>1</sub> and M<sub>2</sub>, the mesencephalic segments; N. III, Nervus oculomotorius; P, Parencephalon; r. m<sub>2</sub>—mt, the boundary-ridge between the Mes- and Metencephalon; r. s-m., the boundary-ridge between the Syn- and Mesencephalon; S, Synencephalon; S. i. p., Sulcus intraencephalicus posterior; T, Telencephalon; T. p., Tuberculum posterius.

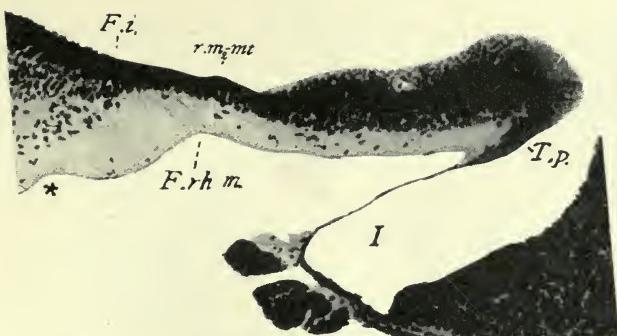


Fig. 26.

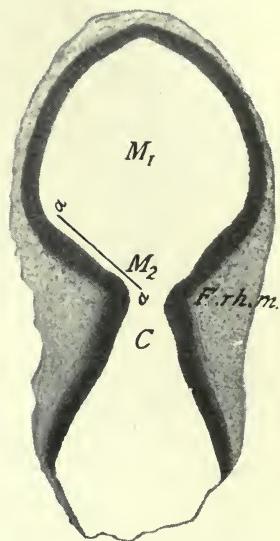


Fig. 29.

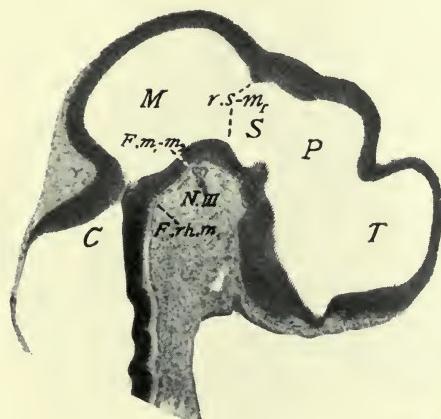


Fig. 27.

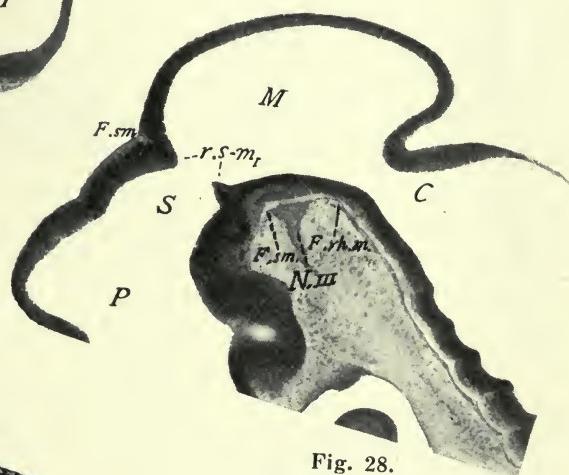


Fig. 28.

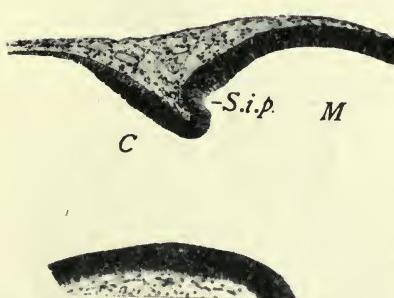


Fig. 30.

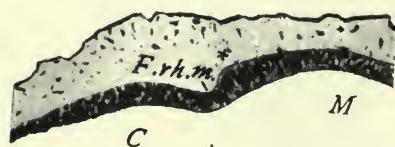


Fig. 31.

The anterior mesencephalic segment is, in other words, more laterally expanded in *Gallus* than in the corresponding *Acanthias* stages. That the posterior lesser concavity forms Sulcus intraencephalicus is clearly seen at later stages. (The anterior mesencephalic segment of KAMON [1906] [Figs. 1 and 2] appears to me to be identical with the segment D Fig. 3 and 4, comp. also HILL [1899].)

Already at the stage of 50 hours, a distinct little depression of the Tectum has formed immediately dorsal to and in front of Velum medullare anticum (S. i. p. Fig. 30). This depression is also to be found at the 60 hours stage. Partly in sagittal sections, and partly in total preparations, Sulcus intraencephalicus can be proved to be connected with this recess, which thus constitutes a dorsal connection between the lateral Sulci intraencephalici. A similar dorsal part of Sulcus intraencephalicus is to be found in *Rana* at, e. g. stage 3,0 cm. Here however Sulcus intraencephalicus is dorsally not nearly so well-defined as in *Gallus*. In other types I have not been able to establish any medial dorsal part of the posterior segment (Sulcus intraencephalicus). In *Acanthias*, however, at stages 1,5—2,7 cm., in a medial longitudinal section, the hindmost part of the Tectum is nevertheless, seen to be distinctly thickened (\* Fig. 31). Apart from the fact that this thickening is devoid of a cavity, this part greatly resembles the dorsal part belonging to the M<sub>2</sub>-segment in *Gallus* (comp. Fig. 30 with Fig. 31). I do not therefore endorse HERRICK's (1917) opinion, when he says that Sulcus isthmi (Sulcus intraencephalicus) in *Amblystoma* can be followed in a dorsal direction "to end in the Recessus posterior mesencephali").

At the stages of 4 and 4½ days of *Gallus*, the roof of the Diencephalon is seen subdivided into three parts instead of two, as is usually the case (Fig. 32). The foremost part belongs to the Parencephalon. Behind this, on the boundary to the central part, lies the oriment of the Epiphysis (E. Fig. 32). Between the Epiphysis and Tectum lie two parts separated by a

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Fig. 32. Sagital section of *Gallus* at the 4 day stage. Fig. 33. Parasagital section of *Mus* at stage 0,5 cm. Fig. 34. Parasagital section of *Mus* at stage 0,8 cm. Fig. 35. Parasagital section through the posterior part of the mid-brain of *Acanthias* at stage 5,5 cm. Fig. 36. Transverse section through the posterior part of the mid-brain of *Mus* at stage 1,0 cm. Fig. 37. Sagital section through the ventro-medial part of the mid-brain of *Mus* at stage 0,5 cm. (Microphotographs.)

b. M., the bundle of Meynert; C, Cerebellum; C. p., Commissura posterior; D. c., the dorsal part and column; E, Epiphysis; E. i., Eminentia interpeduncularis; F. i., Fovea isthmi; F. m<sub>1</sub>-m<sub>2</sub>, the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; I, the infundibular region; M, Mesencephalon; M<sub>1</sub> and M<sub>2</sub>, the mesencephalic segments; P, Parencephalon; P. i., Pars intercalaris; R. p. m., Recessus posterior mesencephali; S, Synencephalon; S. i. p., Sulcus intraencephalicus posterior; S. l. t., Sulcus lateralis tecti; T, Telencephalon; T. o., Tectum opticum; Z, the boundary-zone between the Mes- and Metencephalon.

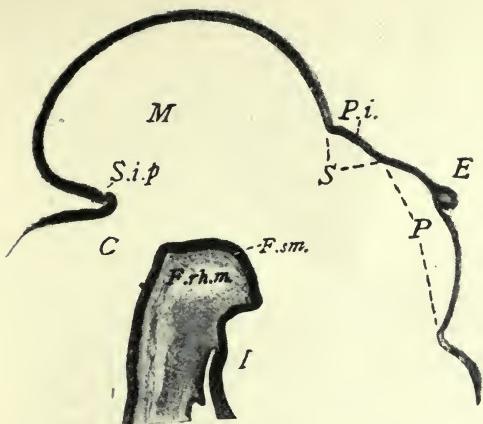


Fig. 32.

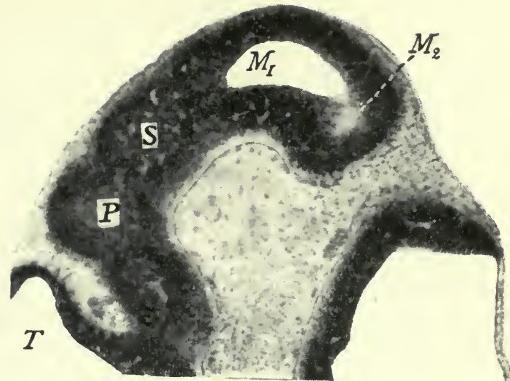


Fig. 33.

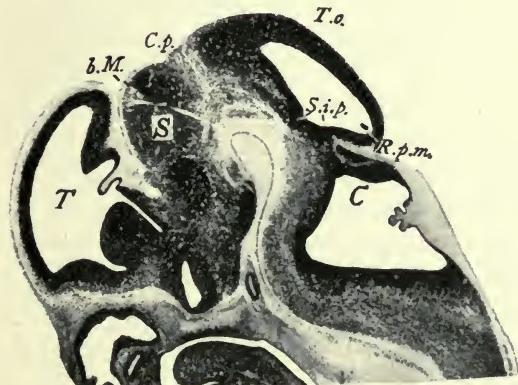


Fig. 34.

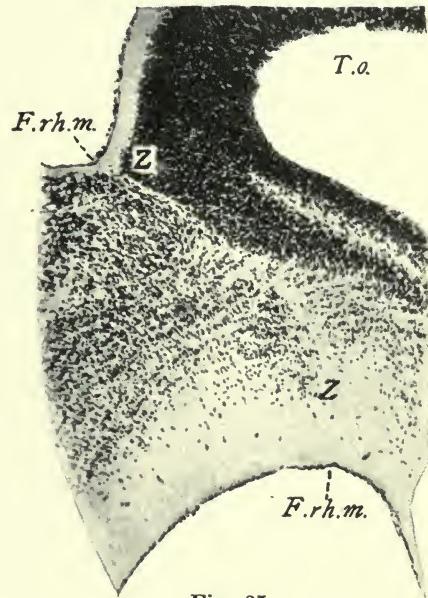


Fig. 35.

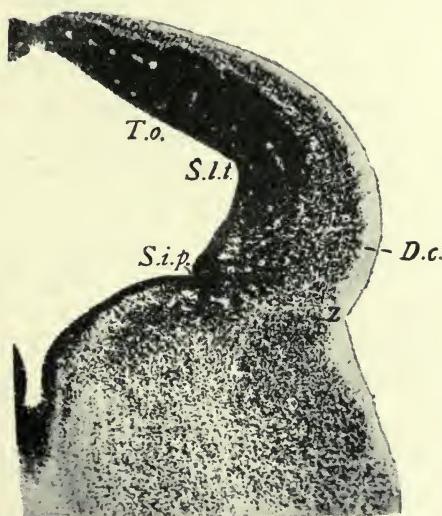


Fig. 36.

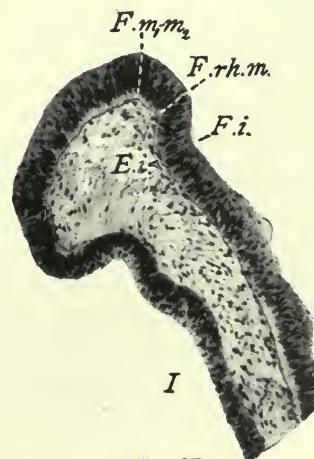


Fig. 37.

well-defined groove. It can now, at somewhat older stages, 5—6 days, be seen that the whole of the central part becomes continually pushed upwards into a perpendicular position, and is included in the formation of the Epiphysis. The hindmost part clearly constitutes the Synencephalon-segment. It is in this part alone that commissural-fibres develop. (comp. KAMON [1906] Fig. 17).

Corresponding conditions clearly exist also among Reptiles (TANDLER AND KANTOR [1907] Fig. 3, Taf. 40, 41). It appears to me very probable, that it is the hindmost of these three diencephalic parts, therefore in reality the roof of the Synencephalon, that KUPFFER (1893, 1905) denoted as the anterior lesser Mesencephalon-segment in *Tropidonotus* and ducks. Commissura posterior would hardly be developed at so early a stage of *Tropidonotus* as that figured and described by KUPFFER. A mistake in regard to the position of the commissure could therefore easily have occurred.

#### F. Mammalia (*Mus musculus* var. *albino*).

The segmentation of the mammalian brain has been described by ZIMMERMANN (1891) and FRORIEP (1892). According to FRORIEP two segments belong to the 'tween-brain and three to the mid-brain. If we assign two segments to the mid-brain, the number of diencephalic segments should be three. Even in *Mus musculus* var. *albino* these three diencephalic segments are discernable (Fig. 33). To the first diencephalic "segment" I have found no corresponding part in lower animals.

At stage 0,5 cm. of *Mus* the posterior mesencephalic segment is so distinctly developed that it appears on a parasagittal section in the same manner as in *Acanthias* at stage 1,5—1,8 cm. (M<sub>2</sub> Fig. 33). The anterior segment M<sub>1</sub> is at this stage considerably larger than the posterior, and rather extended in length; between the segments lies a well-defined boundary-ridge. Of the caudal mesencephalic segment's inner concavity is formed a typical Sulcus intraencephalicus posterior, which at stage 0,8 cm. is deepest and best-defined (S. i. p. Fig. 34). Later, at stages 1,0 to 1,6 cm., this groove grows together more and more, to vanish altogether at last. At these later stages the part where the fusion takes place is marked by a distinct ependymal-cell thickening, from which a relatively cell-free zone (ependymal-fibre zone?) stretches to the surface of the brain, or Fissura rhombo-mesencephalica (z. Fig. 36). A similar zone also exists in *Acanthias* (z. Fig. 35) and *Gallus* (z. Fig. 99) at certain stages. As long as Sulcus intraencephalicus remains, it extends dorsally about as far as in *Acanthias*.

On medial longitudinal sections of stage 0,5 cm. (Fig. 37), two outer grooves, about equally well-developed, are discernable, of which the posterior

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(F. rh. m. Fig. 37) lies immediately in front of Fovea isthmi (F. i. Fig. 37) and thus is Fissura rhombo-mesencephalica (comp. GRÖNBERG'S [1901] stage A of *Erinaceus* Fig. 24 b, c). The anterior of these grooves (F. m<sub>1</sub>—m<sub>2</sub> Fig. 37) must be the boundary-groove M<sub>1</sub>—M<sub>2</sub>. That this is the case appears, firstly, from the posterior mesencephalic segment's concavity, in other words, Sulcus intraencephalicus, (which however, does not reach as far down as to the medial plane) lying between the latter and Fissura rhombo-mesencephalica; secondly from a comparison with the corresponding stage (2,0 cm.) in *Acanthias* (Fig. 10). (In determining the position of Sulcus intraencephalicus, as also in the comparison with *Acanthias*, good help is afforded by the eminence [Eminentia interpeduncularis of His] [E. i. Figs. 11, 12, 16. 37—39] corresponding with the Fovea isthmi [F. i. in the Figs.], with its characteristic arrangement of cells: as in *Acanthias* at stage 2,7 cm. [Fig. 11], the peripheral layer of fibres is fairly broad in segment M<sub>1</sub>, comparatively thin in segment M<sub>2</sub>, and completely lacking under the Fovea isthmi [comp. Figs. 11 with 38]). At a slightly later stage (0,6 cm.) (Fig. 38) the boundary-groove M<sub>1</sub>—M<sub>2</sub> (F. m<sub>1</sub> m<sub>2</sub> Fig. 38) has, as in *Acanthias* at stage 2,7 cm. (Fig. 11) become the best-defined of the two grooves in question. At this stage and at stage 0,55 cm. a faint concavity, i. e. a ventral connecting part of Sulcus intraencephalicus has formed ventrally on the floor of the posterior mesencephalic segment. This concavity soon disappears again, however. At stage 0,7 cm. it has definitely vanished. At stage 0,6 cm. (Fig. 38), which may be compared with stage 2,7 cm. in *Acanthias* (Fig. 11), the Fissura rhombo-mesencephalica can still be clearly distinguished from the boundary-groove M<sub>1</sub>—M<sub>2</sub>. Stage 0,7 cm. (Fig. 39) can be compared with stage 5,5 cm. in *Acanthias* (Fig. 17) Fissura rhombo-mesencephalica and the boundary-groove M<sub>1</sub>—M<sub>2</sub> lie so close together, that they almost form a single groove (Fossa interpeduncularis of His).

It is necessary in *Mus* also to distinguish a Sulcus intraencephalicus from a Fovea isthmi, both of which are found simultaneously and distinct from one another at stage 0,6 cm. The latter disappears later, at the same time as the Sulcus longitudinalis ventralis in its entirety grows together, and is thus not to be found at later stages, as is the case in lower vertebrates.

## 2. THE MORPHOLOGICAL DELIMITATION OF THE MID-BRAIN.

In drawing up the boundary-lines, I have first and foremost sought to determine the natural boundaries between the different parts. A boundary-definition ought further to be such that it can apply to all the vertebrates. As the same number of segments are similarly developed in all the vertebrates, it should be possible to consider the boundaries between these seg-

ments as natural and homologous for all vertebrates. It is clear that the boundary between two segments cannot be fully expressed by a straight line (in e. g. a medial sagittal section), as the boundary is a surface. It is, a priori, to be expected, that during the process of development, a boundary plane, which from the beginning is level, becomes more or less curved, as some parts develope more than others. It is thus clearly impossible in such a case that boundary-grooves and corresponding interneuromeric ridges should alone suffice. Straight lines drawn up between these (on sections) are boundary-lines only in case of the boundary-surface being level. If this surface later becomes curved, these lines become entirely artificial, and only approximate as boundary-lines.

In young embryos the cells lie more or less distinctly arranged in rows, which radiate from the ventricle. Ependymal-fibres also radiate in the same direction so far as I could discover in Golgi- and Haemalum-preparations, in which latter ependymal-fibres can often be traced<sup>1</sup>. Parallel with these there lies a number of lesser blood-vessels. A natural boundary should therefore run parallel to the rows of cells, ependymal-fibres and in certain cases blood-vessels.

#### A. The Boundary between the Mes- and Metencephalon.

The boundary between the Mes- and Metencephalon is marked, partly by Fissura rhombo-mesencephalica and the boundary-ridge corresponding with it; partly by Sulcus intraencephalicus posterior or the ependymal-thickening which remains after this Sulcus has disappeared<sup>2</sup>.

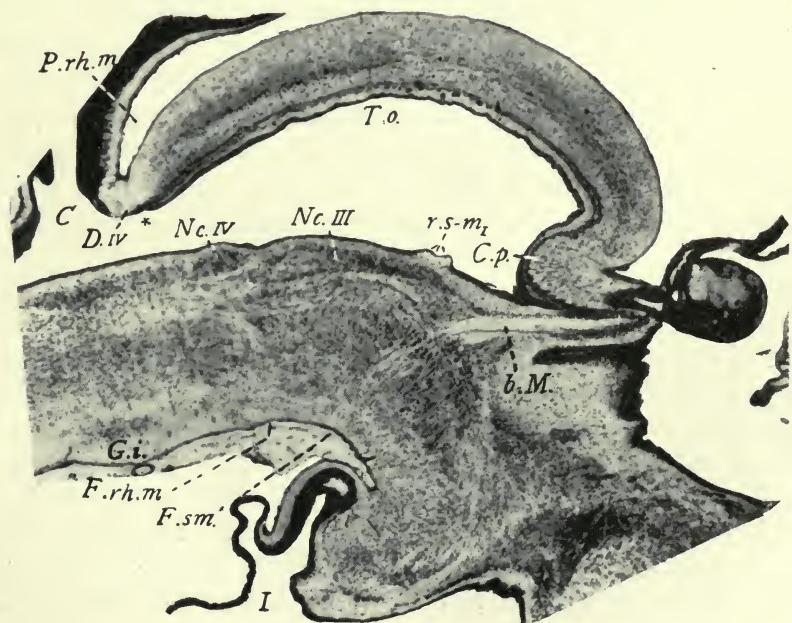
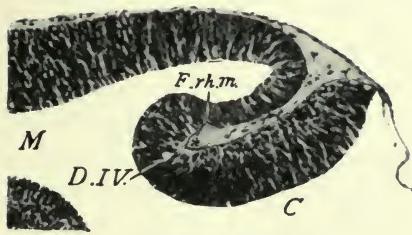
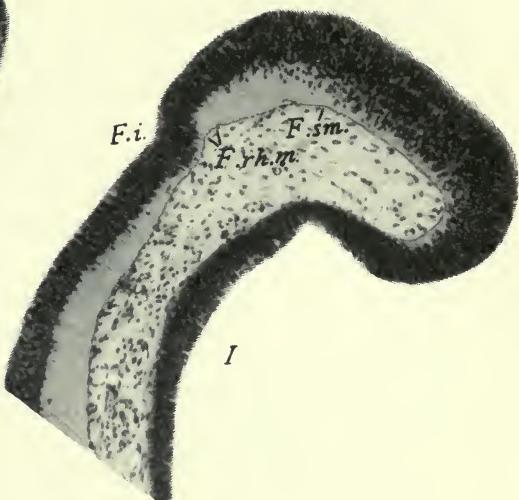
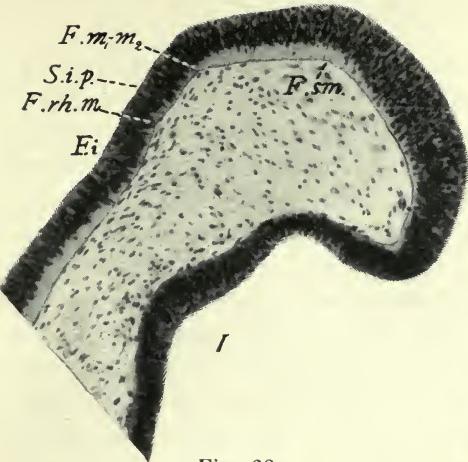
<sup>1</sup> Comp. BURCKHARDT (1891): "In diesem beinahe geometrischen Gerüst von Stützsubstanz (in the mid-brain of *Triton*) gleiten die Neuroblasten peripheriwarts; die neugebildeten lehnen sich jedes Mal an die vorherigen an; so entstehen Reihen von Ganglienzellen, welche in gewissen Stadien durchs ganze Centralnervensystem zu erkennen sind, bedingt durch die Stützsubstanz." See page 378.

<sup>2</sup> As has already been mentioned, Sulcus intraencephalicus posterior can practically be said to lie in the boundary-plane between the Mes- and Metencephalon.

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Fig. 38. Sagital section through the ventro-medial part of the mid-brain of *Mus* at stage 0,6 cm. Fig. 39. Sagital section through the ventro-medial part of the mid-brain of *Mus* at stage 0,7 cm. Fig. 40. Parasagittal section of *Acanthias* at stage 15,0 cm. Fig. 41. Sagital section through Cerebellum of *Salmo* at stage 0,8 cm. (Microphotographs.)

b. M., the bundle of Meynert; C, Cerebellum; C. p., Commissura posterior; D. IV, the decussation of Nervus IV; F. i., Fovea isthmi; F. mi-m<sub>2</sub>, the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; G. i., Ganglion interpedunculare; I, the infundibular region; M, Mesencephalon; Nc. III, Nucleus oculomotorius; Nc. IV, Nucleus trochlearis; P. rh. m., Plica rhombo-mesencephalica; r. s-m, the boundary-ridge between the Syn- and Mesencephalon; S. i. p., Sulcus intraencephalicus posterior; T. o., Tectum opticum.



In *Salmo* and *Rana* there emanate from Sulcus intraencephalicus or the ependymal-thickening well-defined ependymal-fibres, which together form a characteristic boundary-line (Figs. 23, 24, 119). These ependymal-fibres, remain up to such late stages, (in *Salmo*, at least up to stage D; in *Rana*, during the whole larva-stage) that a precise definition of the position of the boundary-plane in relation to the cell-structures is made possible. In *Acanthias*, *Gallus* and *Mus* (and also as far as I could make out from the *Iguana* sections available to me, in Reptiles) there is no such boundary-line of thick ependymal-fibres. On the other hand in these species the posterior mesencephalic segment is distinguished by its deficiency in cells, so that from Sulcus intraencephalicus or the ependymal-cell-thickening a comparatively cell-free boundary-zone (z. Figs. 35, 36, 99) can be traced out towards Fissura rhombo-mesencephalica. It is true that in older stages this zone becomes more indistinct or even disappears, but by that time it has generally been possible to determine the position of the boundary-plane in relation to the differentiated structures.

The dorsal part of Fissura rhombo-mesencephalica is in *Acanthias*, at stages 2,0 cm. to 3,9 cm. sharply V-shaped on sagittal sections. Already at the 3,9 cm. stage the decussation of the trochlear nerve is visible as a colourless spot immediately behind this groove. In consequence, it would appear, of the Decussatio veli's increase in size, Plica rhombo-mesencephalica (P. rh. m. Fig. 40) becomes later L-shaped on sections. The anterior of the closely-lying grooves (Fig. 40) is clearly the Fissura rhombo-mesencephalica proper. The decussation of the trochlear nerve (D. IV Fig. 40) lies immediately behind this. (The ventricular groove \* in front of D. IV Fig. 40 has nothing to do with Sulcus intraencephalicus, but develops secondarily at stages 8,0 to 15,0 cm.).

Laterally Fissura rhombo-mesencephalica is at stages 2,7 to 3,8 cm. fairly shallow and vanishes entirely later on.

On a medial longitudinal section of *Salmo*, stage 0,6 cm. (Fig. 19) Fissura rhombo-mesencephalica appears as a well-defined groove between the Tectum and Cerebellum. Behind this groove, at stage 0,8 cm., a new one (\* Fig. 41) has developed. The anterior and upper of these grooves (F. rh. m. Fig. 41) should be the Fissura rhombo-mesencephalica proper. Right inwards to (thus in no case behind) the lower groove, the decussation of the trochlear nerves emerges distinctly at this stage (D. IV Fig. 41). Thenceforth Fissura rhombo-mesencephalica retains its position between the Tectum opticum and Valvula cerebelli, even at stage 1,0 cm., but disappears later completely, dorso-medially. The powerful transformations, which take place in this region in connection with the development of the Valvula cerebelli, cause, so to say, a straightening of that part in which Fissura rhombo-mesencephalica was situated. The angle (Fissura rhombo-mesencephalica)

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which forms between the caudal surface of the Valvula and Tectum, at stage 0,8 cm., becomes in other words more and more obtuse, till it entirely disappears. At later stages, in spite of this, it is quite easy, to define the boundary between the Valvula and Tectum in consequence of the differing structure of these parts.

Fissura rhombo-mesencephalica remains ventrally sharp and well-defined up to stage 1,0 cm. (F. rh. m. Fig. 21). At this stage another distinct groove (\*\* Fig. 21) lies behind Fissura rhombo-mesencephalica. At stage 1,1 cm. this caudal groove remains, while the Fissura rhombo-mesencephalica has totally vanished<sup>1</sup>. A homologon to the groove \*\* Fig. 21, is developed 1) in *Acanthias* at stages 6,5—15,0 cm. (\* Fig. 42); 2) in *Rana* at stage 3,6 cm. (\* Fig. 26); 3) in *Gallus* at the stage of 15 days, (possibly earlier), and in *Mus* at stage 1,0 to 2,3 cm. In all these species, the groove lies immediately in front of Ganglion interpedunculare (the greater cellrich part of this Ganglion), develops comparatively late, and is therefore, highly probably homologous. In *Salmo*, during stages B and D, the distance between the groove and the bunch of cells becomes somewhat shortened, so that an erroneous interpretation of this groove as Fissura rhombo-mesencephalica can easily be made.

In *Rana*, as in *Gallus* and *Mus*, the ventro-lateral part of the Fissura rhombo-mesencephalica is very slight and vanishes soon completely. Dorsally, the Plica rhombo-mesencephalica in *Rana* is well-defined up to stage 1,5 cm. and becomes later L-shaped (stage 3,0 cm.). The part between the two angles or grooves (Velum medullare anticum) becomes later more and more fronto-caudally extended (Figs. 24, 96). It is easy by means of the position of the boundary-zone to determine that the foremost of these angles is the Fissura rhombo-mesencephalica. The position of the decussation of the trochlear nerve is difficult to define in *Rana*-larvae.

In *Mus* on the contrary, where the fold between the Cerebellum and Tectum (Plica rhombo-mesencephalica) soon appears L-shaped on sections, it is possible, e. g. at stage 0,6 cm. to determine with certainty that the decussation of the trochlear nerve lies behind the Fissura rhombo-mesencephalica. This groove, which thus bounds the Velum medullare anticum frontad, as well as the posterior groove or angle, which bounds the Velum

<sup>1</sup> It is to be noticed, that from the Sulcus intraencephalicus and Fovea isthmi issues, in a ventral direction, a pointed plug of cells, which at stage 1,0 cm. lies right inwards to the Fissura rhombo-mesencephalica, but at stage 1,1 cm., a good distance in front of the now sole remaining groove. This characteristic plug of cells (which KUPFFER [1905] figures in Fig. 149), should be considered homologous with the cell-mass, which in *Acanthias*, at certain corresponding stages (2,7—3,2 cm.) lies under the Fovea isthmi and extends at certain stages to the ventral surface of the brain (compare page 23). A similar cell-arrangement has been described by BURCKHARDT (1892) in *Triton* and by KINGSBURY (1895) and HERRICK (1917) in *Necturus*.

caudad towards the Corpus cerebelli, remains very well-defined' in all investigated embryonic stages. This is not the case with *Gallus*, where Fissura or Plica rhombo-mesencephalica becomes U-shaped. At the stage of 4 days, however, it can with certainty be proved that the trochlear-decussation lies behind the Fissura rhombo-mesencephalica. With the depression of the medial part of the Tectum, Fissura rhombo-mesencephalica disappears dorsally entirely.

There is no indication of the Fissura rhombo-mesencephalica ventro-medially in *Rana* at stages 0,5 to 3,0 cm. or in *Gallus* at the 50 hour-stage. At stage 3,0 cm. in *Rana* there lies however a groove in such a position in relation to the Sulcus intraencephalicus and Eminentia interpeduncularis, that it may be defined as Fissura rhombo-mesencephalica (F. rh. m. Fig. 25). The stage 3,6 cm. corresponds with the 1,0 cm. stage in *Salmo*, in so far as that a groove (\* Fig. 26) has developed behind the Fissura rhombo-mesencephalica. This caudal groove is found again in post-larval brains immediately before the Ganglion interpedunculare. The Fissura rhombo-mesencephalica has at these stages again become obliterated.. In *Gallus* there soon develops (stages 60 hours etc., Fig. 32) a very clear and well-defined ventral part of the Fissura rhombo-mesencephalica which remains at least to the 15 day stage. I do not therefore agree with KAMON (1906) when he says, that in the 94 hour stage (Embryo VII) "vorn oder hinten keine äussere Grenzfurche findet" (page 607).

It is evident from the above, that the Trochlearis-decussation lies immediately behind the boundary between the Mes- and Metencephalon. This is also the case with the lateral Trochlearis-tracts, which can be followed from the decussation to the Nucleus IV. This is most easily demonstrated, e. g. in *Salmo*: stage 0,6 cm., and in *Gallus*: the 6 day stage, where the Trochlearis-tracts are visible on haemalum preparations as white streaks in the embryonic cell-mass. As the Trochlearis-nucleus lies in the Isthmus region in all the investigated animals, so the Nervus IV, with its nucleus lies altogether outside and behind the Mesencephalon, a fact which has already frequently been pointed out by HIS and other embryologists. In like manner Ganglion interpedunculare undoubtly lies in the Metencephalon (HIS).

#### B. The Boundary between the Syn- and Mesencephalon.

It is comparatively easy to define the caudal boundary of the mid-brain by means of the rudiment of the Sulcus intraencephalicus, Fissura rhombo-mesencephalica, Fovea isthmi and, in *Rana* and *Salmo* also by the "boundary-zone".

It is considerably more difficult to draw up definite boundary-lines between the Syn- and Mesencephalon. In the earlier stages we are chiefly

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obliged to rely on the boundary-groove and the corresponding ridge. In the following I term the boundary-groove: Fissura syn-mesencephalica. (This boundary-groove is not, as I have pointed out above, identical with the Fissura proso-mesencephalica nor with the Fissura dia-mesencephalica).

The boundary between the 'tween-brain and the mid-brain is, as is known, generally drawn from the Commissura posterior down to (HIS) or immediately behind (KUPFFER) Tuberculum posterius. In the following I shall try to shew that this boundary-line is artificial and approximative.

The Fissura syn-mesencephalica is, in the earlier stages of *Acanthias* (e. g. 1,5 cm.) only a faint convex curve between segments S and M<sub>1</sub>. Fig. 43 represents a parasagittal section (5 sections à 10  $\mu$  to the side of the medial plane) of the 1,5 cm. stage. Guided by the boundary-groove and especially by the boundary-ridge, it is possible to draw up the boundary-line. If the series of sections is followed from this section in a medial direction, the position of the Fissura syn-mesencephalica can be approximately determined on the medial section.

It is further clear, that the boundary between the Par- and Synencephalon should be drawn from the posterior edge of the oriment of the Epiphysis (E. Fig. 43) down to the caudal edge of the hypothalamic depression, thus where the Fissura proso-mesencephalica surrounds the brain (comp. Figs. 2, 3, 43).

The boundary-ridge S—M<sub>1</sub> is sharply-defined and clear at stage 1,5 cm. At later stages considerable transformations take place in the Synencephalon. On comparing the parasagittal sections of stages 1,5, 2,7 and 3,2 cm. (Figs. 43, 50, 44) it appears that the dorso-lateral part of the Synencephalon thickens so that the dorsal part (Pars intercalaris [P. i. Figs. 44, 50]) in parasagittal sections, from having been curved outward at stage 1,5 cm. finishes by becoming curved inward at stage 3,2 cm. A more lateral parasagittal section (Fig. 45) of this later stage touches, in consequence of these transformations, a secondary "boundary-ridge" (Prominentia dia-mesencephalica of the authors) which will be found in the middle of the Synencephalon-segment (P. dm. Fig. 45). On the section Fig. 45, the primary boundary-ridge (r. s—m<sub>1</sub>) is, however, also visible, ventrally and dorsally intersected. In consequence of the position of the primary true boundary-ridge in relation to the structural features, I have drawn the conclusion, that the boundary between the Syn- and Mesencephalon runs immediately behind the Commissura posterior, along the sharply-defined line formed frontad by the Tectum-cell-mass, and down to a point which for the present can be said to lie directly in front of the oculomotor-fibres (NEAL [1898]).

It is from several points of view unsuitable to draw the boundary-line down to the Tuberculum posterius. Without going into the question of the position of the Tuberculum posterius in relation to the diencephalic segments,

I will only point out that in any case it lies far in front of the primary boundary-ridge between the Syn- and Mesencephalon (see Figs. 2, 3, 43). A line drawn from the Commissura posterior to the Tuberculum posterius would go obliquely through the Synencephalon. KUPFFER (1905) and others have therefore assigned Tuberculum posterius to the Diencephalon, without however determining the position of the boundary plane more closely.

At stage 15,0 cm., in the ventral part of the now bipartite Tuberculum posterius, a number of lymphatic cavities (v. Fig. 42) have been formed under the ependymal layer, so that the point of this part becomes vacuolated. The same curious structure is to be found in the Tuberculum posterius in *Petromyzon* and *Ammocoetes*. (Comp. also below p. 34).

Figs. 47—50 represent parasagittal sections from a series of sagittal sections of stage 2,7 cm. Guided by the position of the primary boundary-ridge, the boundary-line can be drawn as the line in Fig. 50. In the basal part the cell-layers form an angle, whose apex lies in the boundary-ridge. This arrangement of cells is found again in more laterally lying sections (Figs. 49, 48), where the boundary-plane is marked by a straight line in the cell-mass. Still more laterally (Fig. 47) it is tangent to a dorso-ventral system of fibres, whose anterior part consists of the bundle of MEYNERT (b. M. Figs. 47, 51) and the posterior part of the Commissura posterior-fibres (C. p. Figs. 47, 51). The hindmost of these fibres lie close to the line which the Tectum-cell-mass forms in front and can thus be said to form semicircles in the boundary-plane. The bundle of MEYNERT runs obliquely downwards in a ventro-caudal direction and converges with the Commissura posterior-fibres. (The part between the Synencephalon-cell-mass [S. Figs. 47, 48] and the Mesencephalon corresponds to the secondary boundary-ridge. As the embryonic cell-mass is less compact in the periphery, and as a parasagittal section cuts deepest into the cell-mass S and M [Figs. 47, 48], thus giving the part that lies between, the appearance of a separate segment).

It is thus shewn that the boundary-plane is determined by the structural features themselves, and must therefore be looked upon as a natural boundary-

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Fig. 42. Sagittal section through the ventral part of the brain of *Acanthias* at stage 15,0 cm. Fig. 43. Parasagittal section of *Acanthias* at stage 1,5 cm. Figs. 44, 45. Parasagittal sections through the Synencephalon of *Acanthias* at stage 3,2 cm. Fig. 46. Sagittal section of *Acanthias* at stage 3,9 cm. (Microphotographs.)

C, Cerebellum; C. p., Commissura posterior; E, Epiphysis; F. i., Fovea isthmi; F. m<sub>1</sub>-m<sub>2</sub>, the boundary-groove between the mesencephalic segments; F. rh. m., Fissura rhombo-mesencephalica; F. sm., Fissura syn-mesencephalica; G. i., Ganglion interpedunculare; I, the infundibular region; M, Mesencephalon; P, Parencephalon; P. d. m., Prominentia dia-mesencephalica; P. i., Pars intercalaris; r. s-m<sub>1</sub>, the boundary-ridge between the Syn- and Mesencephalon; S, Synencephalon; T, Telencephalon; T. p., Tuberculum posterius; T. o., Tectum opticum; v, vacuoles in the Tuberculum posterius.

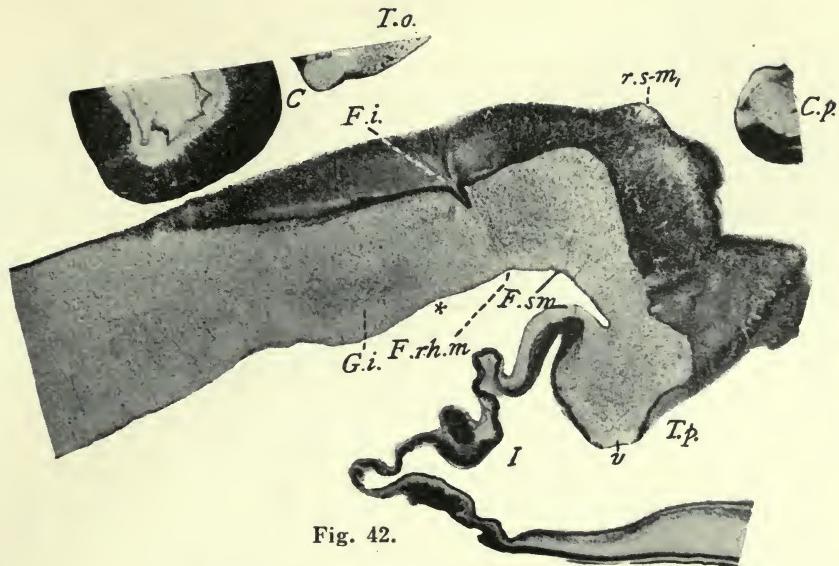


Fig. 42.

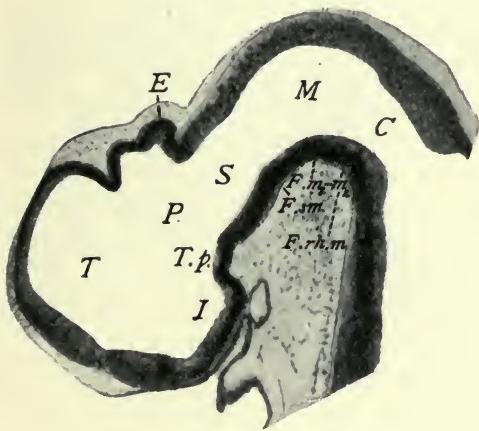


Fig. 43.

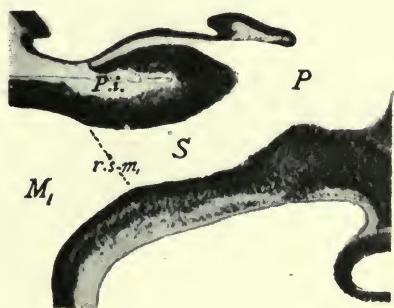


Fig. 44.

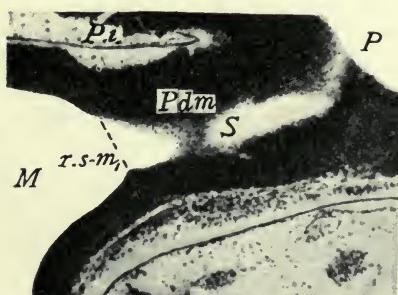


Fig. 45.

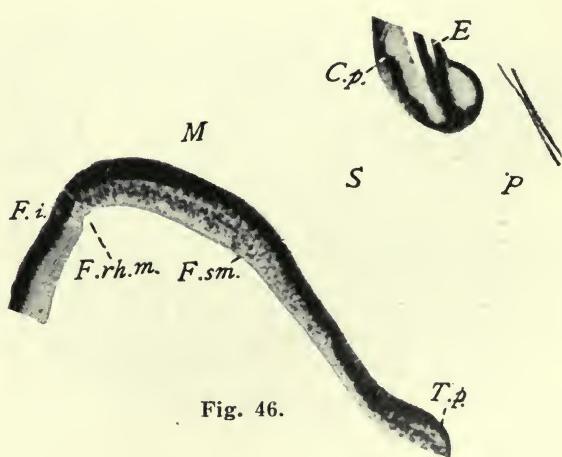


Fig. 46.

plane. Medially to the section Fig. 50 there is also to be found a structural, though not sharply-defined boundary. In the floor of the mid-brain there is a stratum of fibres considerably thicker than in the floor of the Synencephalon where the cell-mass extends almost down to the surface of the brain. Developing later (stage 3,9 cm. etc.) in this mesencephalic fibre-stratum, a cell-mass somewhat more compact than the corresponding one in Synencephalon, is to be found (Fig. 46).

To sum up, it may be said, that the boundary-plane between the Syn- and Mesencephalon is determined by the Fissura syn-mesencephalica and by the position of the primary boundary-ridge. This boundary-plane coincides: 1) with the disappearance of the Tectum-formation in front; 2) with the dorsal and lateral parts of the Commissura posterior-fibres; 3) with the ventro-medial part of the bundle of MEYNERT, i. e. with the point where this bundle bends over in a horizontal direction, and 4) with a point immediately in front of the oculomotor nerve. A more precise definition of the position of the boundary-plane in relation to the structural features is given below (page 46). The boundary-plane thus determined, clearly lies considerably behind the line generally accepted in the literature as the boundary-line between the Di- and Mesencephalon.

In *Salmo* Fissura syn-mesencephalica is not dorsally and laterally developed as a sharply-defined groove at the earliest stages I have had access to (0,6 cm.), and can thus not be traced round the brain down to the ventral side. Four sharply-defined grooves have at this stage (0,6 cm.) developed ventrally. Of these the most caudal is undoubtedly Fissura rhombo-mesencephalica (F. rh. m. Fig. 19). As the posterior mesencephalic segment in *Salmo* at stage 0,6 cm. is already reduced to a groove (Sulcus intraencephalicus posterior) it must be assumed that the boundary-groove M<sub>1</sub>—M<sub>2</sub> here, as in *Acanthias* at stages 3,9 to 5,5 cm., has already approached the Fissura rhombo-mesencephalica and caused the distinct L-shaped appearance, which is to be found also in *Salmo* (Fig. 19). A comparison with an earlier *Acanthias* stage (1,5 cm.) (Fig. 43) and an examination of the series of sections would shew that the two foremost (\*, \*\* Fig. 19) of the above-mentioned four grooves, are identical with those which in *Acanthias* lie directly dorsally to the infundibular depression. One or both of these pro-

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Figs. 47—50. Four parasagittal sections of the same series of *Acanthias* at stage 2,7 cm. Fig. 51. Parasagittal section of *Acanthias* at stage 3,2 cm. (Silver impregnation according to Cajal.) Fig. 52. Sagittal section of *Salmo* at stage D. (Microphotographs.)

b. M., the bundle of Meynert; b. v., the "boundary-vessel"; C, Cerebellum; C. p., Commissura posterior; F. i., Fovea isthmi; F. sm., Fissura syn-mesencephalica; G. i., Ganglion interpedunculare; H, the hypothalamic region; M, Mesencephalon; N. III, Nervus oculomotorius; P, Parencephalon; P. i., Pars intercalaris; P. m. a., Pars medialis auriculi; S, Synencephalon; T. o., Tectum opticum; T. p., Tuberculum posterius; Vl. c., Valvula cerebelli.

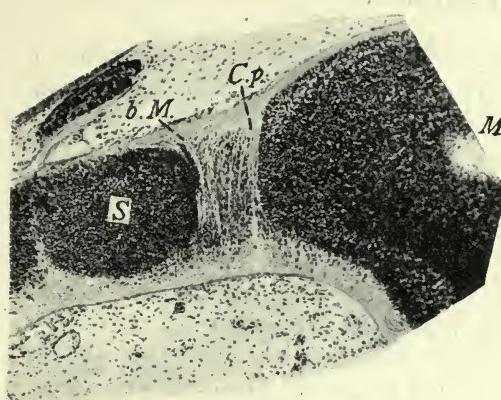


Fig. 47.

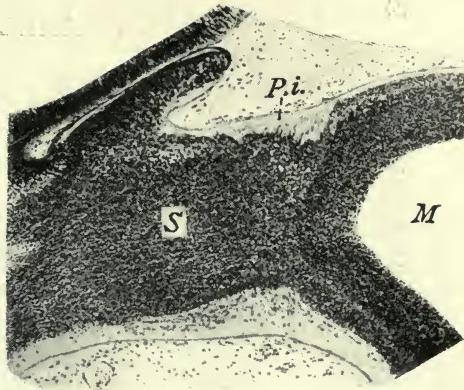


Fig. 48.

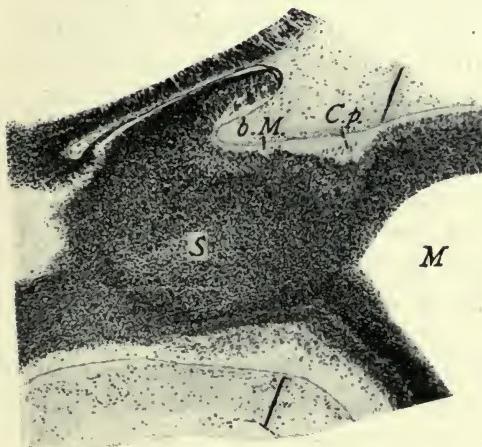


Fig. 49.

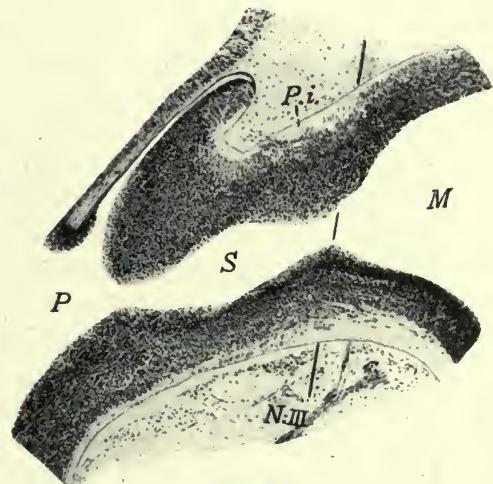


Fig. 50.

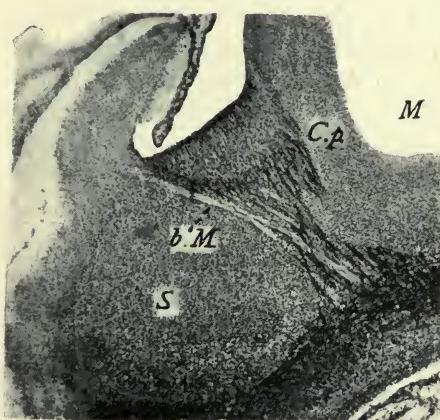


Fig. 51.

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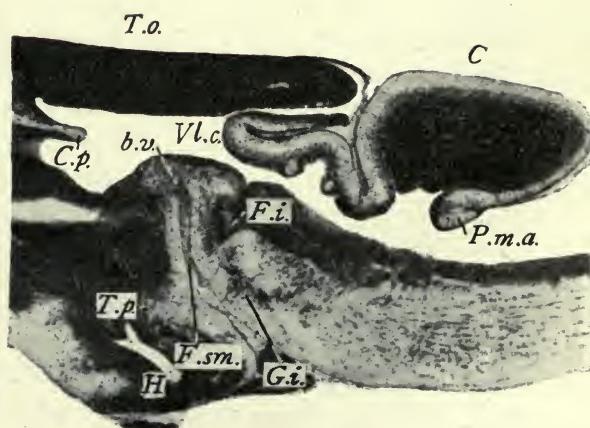


Fig. 52.

bably answer to the original Fissura proso-mesencephalica. There remains then only one groove, which must be the Fissura syn-mesencephalica (F. sm. Fig. 19).

The points of agreement with corresponding *Acanthias* stages are also very marked at later stages. It should here suffice to compare e. g. stage 1,0 cm. of *Salmo* with corresponding stages of *Acanthias*.

In *Salmo*, as in *Acanthias* (up to stage 8,0 cm.), the Tuberculum posterius is undivided, but in *Salmo* it is by this time already vacuolized (v. Fig. 21), as is the case at later stages of *Acanthias* (v. Fig. 42). Right outside the Tuberculum posterius and thus in the place where at stage 0,6 cm. in *Salmo* (Fig. 19) and 1,5 cm. in *Acanthias* (Fig. 43), two grooves were developed dorsally to the infundibular depression, in both cases there is only one groove (comp. Figs. 21, 42) and behind it in *Salmo*, a very sharply-defined groove, the same which has already been assumed to be the Fissura syn-mesencephalica (F. sm. Fig. 21). Towards this groove the bundle of MEYNERT and the Commissura posterior-fibres converge in the same manner as in *Acanthias*. The groove lies also in the prolongation of the line formed frontad by the Tectum-cell-mass. Between this groove and the Fissura rhombo-mesencephalica issues the oculomotor nerve. In relation to the "secondary" boundary-marks, the groove in question thus occupies the same position as the Fissura syn-mesencephalica in *Acanthias*. The only difference being, that the Fissura syn-mesencephalica is very well-defined in *Salmo*, but in *Acanthias*, on the contrary, is particularly faint (F. sm. Figs. 42, 46).

The boundary-plane between the Syn- and Mesencephalon can consequently be determined in the same way in *Salmo*, as in *Acanthias*. As a further help in the work of definition, in the case of *Salmo*, can be used a characteristic blood-vessel (b. v. Figs. 52, 76), which, at an already early stage (0,8 cm.) is clearly developed. It enters the brain ventrally and medially at Fissura syn-mesencephalica, rises later obliquely towards the "Haubenwülste", after which it ramifies into two lateral vessels, which extend dorso-laterally towards the Commissura posterior (comp. FRITSCH [1878]). A study of series of sagital sections of earlier stages shew clearly that this blood-vessel lies in the actual boundary-plane, and thus intersegmentally.

A comparison between the earlier and later stages of *Salmo* shews, that the boundary-plane, during the process of development becomes more and more cup-shaped, with the concave side facing forwards. The anterior part of Tectum grows frontad and over the Commissura posterior, which, seen topographically, thus lies behind and under the same. The floor-part of the mid-brain becomes raised, so that the "boundary-blood-vessel" takes, a nearly upright position (Fig. 52). This curving of the boundary-plane occurs also in *Acanthias*, though in a considerably less degree.

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It is very difficult to compare the ventro-medial part of the Syn- and Mesencephalon in *Rana* with the corresponding parts in *Acanthias* and *Salmo*. To obtain points of contact, it is necessary to take very young embryonic stages (0,5—0,7 cm.) of *Rana*, before the transformations which characterize this species have set in.

In *Rana* at e. g. stage 0,6 cm. the Fissura syn-mesencephalica is circular, and its position on the medial section can consequently be determined (F. sm. Fig. 53). The groove (\* Fig. 53) which lies in front of the Fissura syn-mesencephalica can be traced in a lateral and frontal direction, where it forms the boundary between the hypothalamic region and the remaining part of the Diencephalon. The part which, in the medial section, lies immediately dorsal to the infundibular depression and right opposite this groove, is doubtless *Tuberculum posterius*. Not till stages 3,0 and 3,6 cm., does this part become vacuolized in the same manner as in *Acanthias*.

The distance between the ventral parts of the grooves in question becomes lessened at later stages (0,7—0,8 cm.) till they can no longer be distinguished from each other, in other words, the grooves converge down to the same ventral point (Fig. 54). The whole of the powerful floor-part of the Synencephalon, which in *Acanthias* lies between the Fissura syn-mesencephalica and *Lobus posterior* is thus considerably reduced in *Rana*. At later stages, while the groove \* Fig. 53 remains, the Fissura syn-mesencephalica disappears entirely laterally and ventrally.

In *Rana* the fibres of the bundle of MEYNERT lie so scattered, that they cannot be identified in a haemalum-preparation. The Commissura posterior complex and the Tectum-cell-mass remain however, as good landmarks. The boundary-plane in *Rana* lies very nearly vertical, and almost level in contrast to what is the case in *Acanthias* and *Salmo*.

Neither *Salmo* nor *Rana* are, independently of *Acanthias*, suitable subjects for a study of the boundary-plane between the Syn- and Mesencephalon. *Gallus*, on the contrary, seems in several respects, to be an even more suitable subject than *Acanthias* in this connection. While in *Acanthias* the Fissura syn-mesencephalica is very slightly developed, and it therefore becomes necessary to rely almost entirely on the position of the boundary-ridge when determining the delimitations, in *Gallus* there is besides a distinct Fissura syn-mesencephalica, also a particularly well-defined and clear primary boundary-ridge.

At the stage, during which the Commissura posterior develops (4—5 days) the Fissura syn-mesencephalica is dorsally very well-defined, and lies immediately behind the commissures, which forms the roof of the Synencephalon (Pars intercalaris). The caudal part of this commissural plate is composed of the Commissura posterior (C. p. Figs. 55, 56). The Fissura syn-mesencephalica can, e. g. at the stage of 60 hours — 4 days, be traced on

a series of sagittal sections, in a lateral direction to a section, which is tangent to the very sharply-defined boundary-ridge (r. s—m<sub>1</sub> Fig. 28). On the ventro-lateral side of the brain, the Fissura syn-mesencephalica can still be perceived although faintly, immediately in front of the Nervus oculomotorius (Fig. 28). The stage of 50 hours corresponds with these stages. At older stages (5 and 6 days) transformations take place in the Synencephalon, which cause the formation of a secondary boundary-ridge. The edge of this ridge (Prominentia dia-mesencephalica), lies in front of the primary ridge, or about the middle of the Synencephalon-segment (P. dm. Fig. 56).

The Commissura posterior-fibres, the bundle of MEYNERT and the line which the Tectum cell-mass forms frontad, lie in the same morphological position in relation to the boundary-plane as in *Acanthias*. This is also the case in *Mus*.

In *Mus* there is no boundary-groove between the Syn- and Mesencephalon at the earlier stages (0,5—0,7 cm.). A groove certainly does form dorsally in front of the Tectum through the later growth of the latter (at stages 0,8 cm. and so on), but this groove cannot be considered of the same importance as a boundary-groove as the Fissura syn-mesencephalica, which e. g. in *Gallus* is developed at earlier stages. In *Gallus*, as well as in *Acanthias* and in the other investigated species, a secondary groove, lying opposite to Commissura posterior, develops at later stages, but only in connection with the formation of the secondary ridge (Prominentia dia-mesencephalica). It must have been these completely secondary "Sulcus" and "Prominentia dia-mesencephalica" which have caused the boundary-plane to be generally located right through the Commissura posterior.

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Fig. 53. Sagital section through the ventro-medial part of the mid-brain of *Rana* at stage 0,6 cm. Fig. 54. Sagital section through the ventro-medial part of the mid-brain of *Rana* at stage 0,8 cm. Fig. 55. Parasagittal section through the Synencephalon in *Gallus* at stage 4 days. Fig. 56. Parasagittal section through the Synencephalon in *Gallus* at stage 5 days. Fig. 57. Transverse-section through the mid-brain of *Acanthias* at stage 3,9 cm. Fig. 58. Transverse-section of the mid-brain of *Acanthias* at stage 5,0 cm. (Microphotographs.)

C. p., Commissura posterior; D. c., the dorsal part and column; F. l. d., Fasciculus longitudinalis dorsalis; F. sm., Fissura syn-mesencephalica; F. rh. m., Fissura rhombo-mesencephalica; I, the infundibular region; L. c., the lateral part and column; M, Mesencephalon; M. c., the medial part and column; m., l., the medial, lateral portion of the part in question; M. o., Medulla oblongata; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; P, Parencephalon; P. dm., Prominentia dia-mesencephalica; P. i., Pars intercalaris; p. nc., the peripheral nucleus in the lateral part; S, Synencephalon; S. c. e., Stratum cellulare externum; S. c. i., Stratum cellulare internum; S. e., Stratum ependymale; S. l., Sulcus lateralis; S. l. v., Sulcus longitudinalis ventralis; T. f., the Torus-formation; T. o., Tectum opticum; T. p., Tuberculum posterius; V. c., the ventral part and column; vl, the ventro-lateral portion of the ventral column.

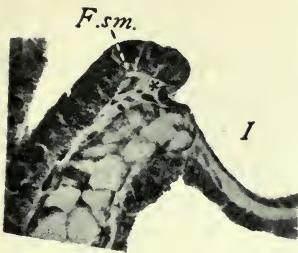


Fig. 53.

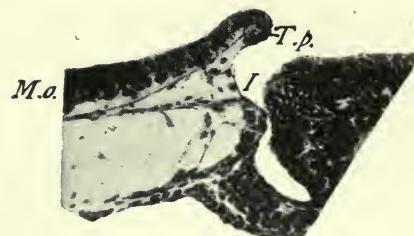


Fig. 54.

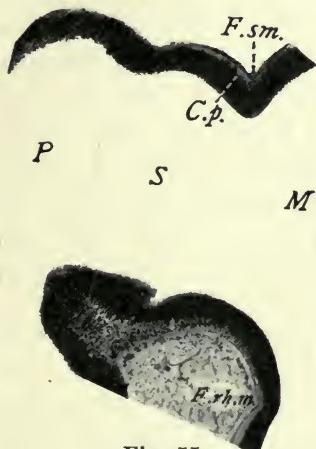


Fig. 55.

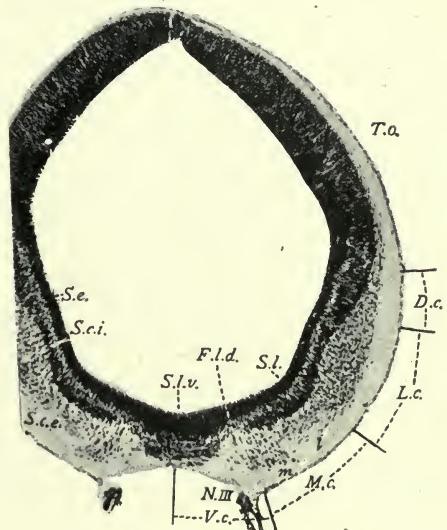


Fig. 57.

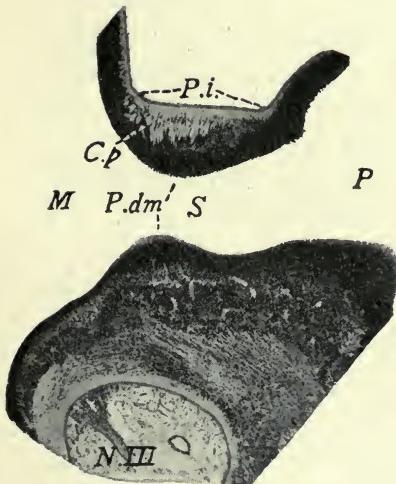


Fig. 56.

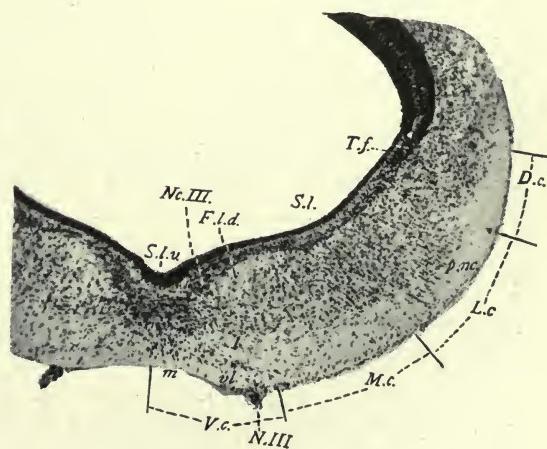


Fig. 58.

TANDLER AND KANTOR (1907) denominate the two ventral angles of the cranial flexure of *Gecko* embryos respectively "vordere" and "hintere Scheitelkrümmung". In stage I., a ridge "Prominentia dia-mesencephalica" proceeds from "vordere Scheitelkrümmung". The same remains in stages II. and III., where, however, Sulcus and Prominentia dia-mesencephalica are only developed dorsally and dorso-laterally. The distance between "vordere" and "hintere Scheitelkrümmung" becomes lengthened in these stages.

In stage IV., on the other hand, Sulcus and Prominentia dia-mesencephalica are directed towards "hintere Scheitelkrümmung"! This peculiar change of position may, perhaps, be accounted for in the following manner. In stage I. (Figs. 1 and 2 of TANDLER), Pars synencephalica has not yet been formed. The groove represented in this stage is evidently identical with Fissura proso-mesencephalica. The groove that subsequently divides the Syn- from the Mesencephalon, at all events in *Gallus*, goes down to a point that is somewhat behind the "vordere Scheitelkrümmung". Judging from TANDLER'S Figs. 3 to 6, the same seems to be the case with *Gecko*. Owing to the distance between the Fissura rhombo-mesencephalica and the Fissura syn-mesencephalica subsequently becoming shorter, not only in *Gallus* but also in all those types of animals subjected by me to examination, the boundary-plane S—M<sub>1</sub> like the boundary-plane M—Mt proceeds from almost the same ventral point.

The base of the Mesencephalon thus becomes very short, more especially in birds and mammals.

In a later work on the development of the brain in *Tarsius*, TANDLER AND FLEISSIG (1915) appears to have assigned the Synencephalon to the mid-brain.

### 3. THE EMBRYOLOGICAL DEVELOPMENT OF THE NUCLEI.

Outside the thick cell-mass, which in young embryos (e. g. *Acanthias*) forms the walls of the brain, a cortical layer of fibre-matter soon develops. The cell-layer (the neuroblastic layer) differentiates later into two layers, an inner: Stratum ependymale (S. e. Fig. 57), and an outer: Stratum cellulare internum (S. c. i. Fig. 57). Cells wander out from the cell-layers into the cortical layer and there form a Stratum cellulare externum (S. c. e. Fig. 57).

The histological structure of the Tectum and of the basal parts not being identical, it is necessary to distinguish between a dorsal part: Tectum mesencephalii and a ventral part in Mesencephalon. In the following I name this latter part: Regio subtectalis, or simply Subtectum<sup>1</sup>.

<sup>1</sup> According to EDINGER (1908), by the term Tegmentum is meant "bei den Säugern die ganze graue Substanz, welche dorsal von den aus dem Grosshirn stammenden Fussbahnen liegt", "für die niederen Vertebraten kommt eigentlich der ganze centrale

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The boundary between these parts should clearly be drawn where the Tectum-formation ventrally ceases. The boundary-line would then run, 1) immediately ventral to the point where the mid-brain ventricle has its greatest lateral extension (I term the more or less sharply defined groove which sometimes develops here, Sulcus lateralis tecti); 2) between the Tectum-formation and Torus semicircularis or Nucleus lateralis mesencephali; 3) along the rows of cells and ependymal fibres outwards to the surface of the brain, where the boundary would then be dorsally close beside the optic tract.

### A. Selachii (*Acanthias vulgaris*).

I have examined in detail the development of the nuclei in *Acanthias* at stages: 3,9, 5,0, 8,0 and 15,0 cm.

*Stage 3,9 cm.* (Fig. 57): Stratum ependymale (S. e.) is at this stage in the Tectum (T. o.), considerably thicker than in the Subtectum, where it is only ventrally and medially (as under the Sulcus longitudinalis ventralis [S. l. v.]) somewhat thickened. Stratum cellulare internum (S. c. i.) is likewise broader in Tectum than in Subtectum. This Subtectum layer is subdivided into thicker and thinner parts: it thickens medially and ventrally; and becomes much thinner close to the Fasciculus longitudinalis dorsalis (F. l. d.), only to increase in thickness again dorsally. This latter thickened part extends up to a ventricular longitudinal groove that I name Sulcus lateralis (S. l.)<sup>1</sup>. Dorsally to this groove Stratum cellulare internum decreases again continuously passing over into the corresponding Tectum layer.

Cells have migrated from these different subtectal parts of the Stratum cellulare internum into the fibre-layer, where groups or columns of cells corresponding to these parts, have formed. These columns, and also the parts of the Stratum cellulare internum extend through the whole of the Mesencephalon, from the frontal to the caudal boundary.

Guided by these structures, I have been able to carry out a subdivision of the Subtectum as follows: the part of the Subtectum which lies between the ventro-medial line and an imaginary line drawn directly laterally to the Fasciculus longitudinalis dorsalis and parallel to the spindle-shaped cells which

Abschnitt des Hinter-, Mittel- und Zwischenhirn als Tegmentum in Betracht" (p. 139). In order to obtain a term for the basal part of the Mesencephalon applicable to the lower as well as the higher vertebrates, I have introduced this new appellation "Subtectum".

<sup>1</sup> This groove is not identical with the Sulcus limitans of His. According to His (1893) the Sulcus limitans is to be found in the mid-brain of adult mammalian brains. In *Mus* the Sulcus lateralis tecti is the only remaining groove. When His, however, states the Sulcus limitans of adult specimens not to be the same as in embryos, there appears to me suitable to introduce the new terms Sulcus lateralis and Sulcus lateralis tecti.

radiate towards the surface of the brain, I have called *the ventral part* (V. c.). This part is bounded laterally in certain animals (*Gallus*) and at certain stages by a ventricular longitudinal groove. Between this groove and Sulcus longitudinalis ventralis the ventral part is at times somewhat raised and forms a longitudinal, rounded-off ridge, called "Haubenwulst" (His). The Stratum cellulare internum of the ventral part forms the Nucleus III. A number of cells lie in the fibre-layer forming the ventral cell-column.

I have named *the medial part* (M. c.) that which lies between "Haubenwulst" and Sulcus lateralis, with corresponding parts of the Subtectum. I assign to this part the thickened portion of the Stratum cellulare internum and the part of the Stratum cellulare externum which corresponds with it: the medial column. This is, at certain stages, frequently divided into two parts, a medial and a lateral (M. c., m. and l.).

To *the lateral part* (L. c.) belong the thinner part of the Stratum cellulare internum which lies between the Torus-formation and the medial part, and also a lateral column in the fibre-layer.

Lastly, I assign to the *dorsal part* (D. c.) the Torus-formation (see below) and a corresponding part of the Stratum cellulare externum: the dorsal column.

The ventral part at stage 3,9 cm. (V. c. Fig. 57) is formed of the following parts: medially of a thick Stratum cellulare internum and outside this a fibre-layer in which there as yet are no cells; laterally to the Nervus III (N. III) and outside the Fasciculus longitudinalis dorsalis (F. l. d.) a number of cells issue from the Stratum cellulare internum surrounding the dorsal longitudinal bundle.

No sharp boundary-line can be drawn between these cells and those which radiate from the medial part of the Stratum cellulare internum. The Stratum cellulare externum is formed of considerably fewer cells in the lateral (l. Fig. 57) than in the medial portion (m. Fig. 57) of this part (M. c. Fig. 57).

The lateral column (L. c. Fig. 57) consists of closely-packed cells, in this respect differing from the dorsal column (D. c. Fig. 57), which is less rich in cells. There is however no sharp boundary-line between the lateral and dorsal columns at this stage.

The development of the nuclei is already practically completed at *stage 5,0 cm.* The only real change that takes place at later stages, is that the columns and nuclei become more diffuse and the boundaries in consequence more difficult to distinguish.

A comparison with stage 3,9 cm. is easily made. The Stratum cellulare internum has formed a distinct magno-cellular Nucleus oculomotorius in the ventral part. A small-cellulated cell-agglomeration, which corresponds to the ventro-medial thickened part of the Stratum cellulare internum lies

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between the two Nuclei and Nervi III. The part, relatively deficient in cells, which at stage 3,9 cm., lies ventrally to the Fasciculus longitudinalis dorsalis (F. l. d. Fig. 58) has at stage 5,0 cm. become filled by a cell-mass (l. Fig. 58), whose origin is difficult to determine. There issue to be sure, from the Stratum cellulare internum round the Fasciculus longitudinalis dorsalis, bi-polar cells, which seem to be connected with the formation of this cell-mass. On the other hand however, the cells in the more medial parts are also bi-polar and arranged with their longitudinal axes in a lateral direction. These cells are in complete continuity with the cell-mass just mentioned (l. Fig. 58). It is impossible for me to decide whether these structural features should be interpreted as shewing the formation of this cell-agglomeration to be in part from the medial part of the ventral column.

There are also bi-polar cells, horizontally arranged in the ventro-lateral part of the ventral column (vl. Fig. 58).

The two parts of the medial column are singularly difficult to distinguish from each other, they are almost completely fused. Peripherally in this part lie a few cells, which probably originate from the column in question.

The following transformations have taken place in the parts lying dorsally to the Sulcus lateralis. The first oriment of the Torus semicircularis or, as I will call it the Torus-formation, becomes visible dorsally in the Stratum cellulare internum towards the boundary to the Tectum. The differentiation in the Stratum cellulare internum, which I call the Torus-formation, lies in the lateral (dorsal) part of the Torus semicircularis of higher animals, as best seen in birds (*Gallus*).

The cell-mass lying in the centre of the Torus-formation I name Nucleus lateralis mesencephali. This is like the Torus-formation a differentiated part of the Stratum cellulare internum. On transverse sections the Stratum cellulare internum here forms a little semicircle (T. f. Fig. 58), in which a lesser cell-agglomeration is found, the Nucleus lateralis mesencephali<sup>1</sup>. Outside this formation a cell-condensation in the Stratum cellulare externum is clearly visible, namely, the dorsal column.

Following the series of transverse sections frontad, the dorsal column is seen passing continuously into a greater cell-mass: the oriment of the Corpus geniculatum laterale of the authors, Ganglion geniculatum mediale of WALLENBERG (1907). According to WALLENBERG (1907), the same seems to be the case in *Carcharias*. He writes (page 389): "An Stelle des medialen Anteils des Mittelhirnhaubenkernes liegt bei *Carcharias* eine mächtige Kernsäule mitten im lateralen Längsbündel, die sich frontalwärts

<sup>1</sup> It would be suitable to introduce a more precise definition of the Nucleus lateralis mesencephali than that hitherto used in the literature. If we assign the whole cell-mass occupying the Torus semicircularis to this Nucleus, this will not be homologous in the different animal types, as will be shewn below.

in ventraler Richtung keulenförmig verbreitert und schliesslich mit dem Ganglion geniculatum mediale zusammenfliesst." This "mächtige Kernsäule" appears to be identical with the dorsal column of *Acanthias*. Judging by WALLENBERG's description and illustrations, his "medialer Teil des Mittelhirnhaubenkernes" in *Scyllium* must be synonymous with what I have called the Torus-formation, and his "lateraler Teil des Mittelhirnhaubenkernes" in the same species with the dorsal column in *Acanthias*.

The lateral column remains in the same manner as at stage 3,9 cm. At this part however, the oriment of a peripheral nucleus (p. nc. Fig. 58) can already be discerned.

In Fig. 427 STERZI (1912) gives a transverse section of a 3,6 cm. *Acanthias*-embryo. STERZI has also evidently noticed the cell-condensations, which I have named the dorsal, lateral and medial columns. He calls the lateral column Formazione reticolata; the medial one Nucleo laterale del mesencefalo; but he does not mention the dorsal column. The part between the Sulcus lateralis and Sulcus longitudinalis ventralis he calls Toro semicircolare.

The nucleus, p. nc. Fig. 58, is completely developed at stage 8,0 cm. As no important changes can otherwise be noticed, I pass on to a description of stage 15,0 cm.

*Stage 15,0 cm.:* The cells in the Stratum cellulare internum of the ventral part (V. c. Fig. 59) are more widely diffused than at the preceeding stage and form together with the ventral column (the cells in the Stratum cellulare externum) a diffuse cell-agglomeration between Nervi III. I have not found any specially differentiated nucleus in the vicinity of, and lateral to the oculomotor fibres in *Acanthias*. Such a nucleus however has been described in *Scyllium* by WALLENBERG (1907) under the name of Nucleus ruber. According to STERZI (1909), a "Nucleo rosso" exists close to the Fasciculus longitudinalis dorsalis in *Acanthias*.

The thickening in the Stratum cellulare internum in the medial part (S. c. i. m. Fig. 59) remains distinct. The whole of the medial column (M. c. Fig. 59) is fairly diffused.

The Stratum cellulare internum continues thinly cellulated in the lateral part (S. c. i. l. Fig. 59). Outside the lateral column (L. c. Fig. 59), which in compactness of cells corresponds with the medial, is found a peripheral, well-defined nucleus (p. nc. Fig. 59), identical with that mentioned at stages 5,0 and 8,0 cm.

Dorsal to the latter nucleus, we find the optic tract in the dorsal part. The dorsal, like the other columns, has become more diffuse, but can still be clearly distinguished (D. c. Fig. 59). The Torus-formation (T. f. Fig. 59) has, in the Stratum cellulare internum developed into a very well-defined semicircular structure, in which lies a little nucleus or cell-column (Nucleus lateralis mesencephali [N. l. m. Fig. 59]).

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The boundary to the Tectum is clearly marked by the Stratum cellulare internum being more vigorous and compact in the Tectum than in the Subtectum. In the Stratum cellulare externum a fairly sharply defined boundary is visible between the Tectum-formation (T. o. Fig. 59) and the dorsal column (D. c. Fig. 59).

Before continuing the description of the development of the nuclei, particularly in the caudal parts of the mid-brain, it would be suitable to define *the boundary between the Mes- and Metencephalon* in relation to the already described cell-columns in the Subtectum. In consequence of the boundary-plane lying at about 45 degrees' angle to the direction of the sections, the metencephalic parts first appear ventrally on a series of transverse sections. In more caudal sections the boundary-lines are to be sought more and more dorsally. The reverse is the case for the boundary between the Syn- and Mesencephalon.

On a series of transverse sections of stage 5,0 cm. it is easy to see the one which cuts through the ventral boundary-point. The Fissura rhombo-mesencephalica (Fossa interpeduncularis) is namely so deep ventrally that it even appears on transverse sections of the brain as an inserted cavity (Fs. i. Fig. 60). Further, the ependymal-fibres behind the groove are considerably more vigorous and receive stains better than in the Mesencephalon. Lastly, a Stratum cellulare externum is lacking ventrally in the Metencephalon<sup>1</sup>.

On this section there is in the medial column a relative paucity of cells (see the right side of the somewhat oblique section Fig. 60 M. c.). A cell-agglomeration lying in the corresponding region, a couple of sections further caudad (see the left side of the section Fig. 60 Mt. c.), is considerably richer in cells than the medial column in Subtectum.

Between this metencephalic cell-column and the mesencephalic lateral column, there lies a relatively cell-free zone, identical with that mentioned above as being the rudiment of the posterior mesencephalic segment (more distinct at stage 3,9 cm.). The rudiment of the Sulcus intraencephalicus lies close to the ventricle. The nucleus of the trochlear nerve now emerges ventro-medially to this zone and lies thus in the Metencephalon.

In following the series of sections caudad, we find the boundary-zone and the rudiment of the Sulcus intraencephalicus displaced upwards till the lateral column is replaced by a metencephalic cell-agglomeration or column. On

<sup>1</sup> Comp. KINGSBURY (1920): "It will be seen (Fig. 1-3) that the differentiated floor-plate characterized by the presence of the ependymal layer only and neuroglial processes (neuroglia fibres), often grouped together in parallel radial bundles, terminates at the Fovea isthmi and cephalad of this point, in the floor of the mid-brain, the characteristic arrangement of the floor-plate is lacking, while ependymal, mantle and marginal layers appear." (Page 117.)

certain caudal sections (Fig. 61) the only remains of the Mesencephalon are the Tectum (T. o.) and the dorsal part of the Subtectum (D. c.).

This latter extends right away to the decussation of the trochlear nerve. Its boundary towards the Metencephalon is very pronounced. Stratum cellulare internum is far richer in the Mes- than in the Metencephalon. In Stratum cellulare externum the boundary-zone is distinct; ventral to it the cells lie also considerably more closely packed than in the dorsal part of subtectum, where, especially caudad, Stratum cellulare externum is formed of only a few cells (D. c. Fig. 61). The dorsal part is thus distinguished from the Tectum-formation by the cells of its Stratum cellulare externum being considerably less closely packed, and by the claviform thickening of its Stratum cellulare internum (Fig. 61). Caudally the dorsal column disappears finally altogether in its capacity as a particularly closely packed cell-column.

At stage 15,0 cm. the Torus-formation can be followed through a series of transverse-sections to sections which cut through the ventral part of the boundary-plane, between the Mes- and Metencephalon, where in other words, they are tangent to Fovea isthmi, and where the rudiment of the Sulcus intraencephalicus is found again in the "Haubenwulst". The Torus-formation becomes, further caudally, a fairly broad and closely packed cell-agglomeration (p. T. f. Fig. 62), which like the Torus-formation lies immediately to the boundary between Tectum and Subtectum and is a differentiation in the Stratum cellulare internum. This cell-agglomeration is the same that at stage 5,0 cm. was described as a claviform thickening of the Stratum cellulare internum in the dorsal part of the Subtectum. (At stage 8,0 cm. it is again visible in like manner, but more clearly defined than at stage 5,0 cm.). Again at stage 15,0 cm. the characteristic rudiment of the ventral to this cell-agglomeration, which fills a part projecting into the Sulcus intraencephalicus (r. S. i. p. Fig. 62) is to be found immediately

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Fig. 59. Transverse-section through the mid-brain of *Acanthias* at stage 15,0 cm.  
 Figs. 60, 61. Transverse sections through the posterior part of the mid-brain of *Acanthias* at stage 5,0 cm. Fig. 62. Transverse section through the posterior part of the mid-brain of *Acanthias* at stage 15,0 cm. Figs. 63, 64. Transverse-sections through the anterior part of the mid-brain of *Acanthias* at stage 15,0 cm. (Microphotographs.)

b. M., the bundle of Meynert; C. p., Commissura posterior; D. c., the dorsal part and column; E. m., Eminentia medialis; F. l. d., Fasciculus longitudinalis dorsalis; Fs. i., Fossa interpeduncularis; G. l., Ganglion geniculatum laterale; L. c., the lateral part and column; M. c., the medial part and column; Mt. c., the metencephalic ventral column; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; Nc. IV, Nucleus trochlearis; N. l. m., Nucleus lateralis mesencephali; p. nc., the peripheral nucleus in the lateral part; r. s-m, the boundary-ridge between the Syn- and Mesencephalon; r. S. i. p., the rudiment of the Sulcus intraencephalicus posterior; p. T. f., the posterior part of the Torus-formation; S. c. i., m., l., the medial and lateral part of the Stratum cellulare internum; S. l. v., Sulcus longitudinalis ventralis; T. f., the Torus-formation; V. c., the ventral part and column.

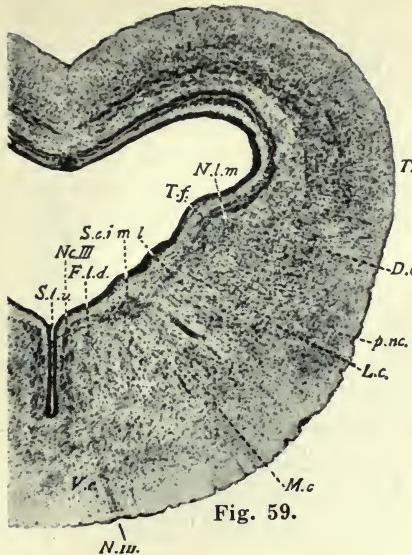


Fig. 59.

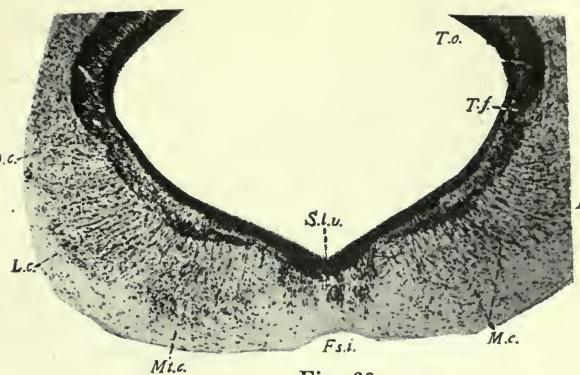


Fig. 60.

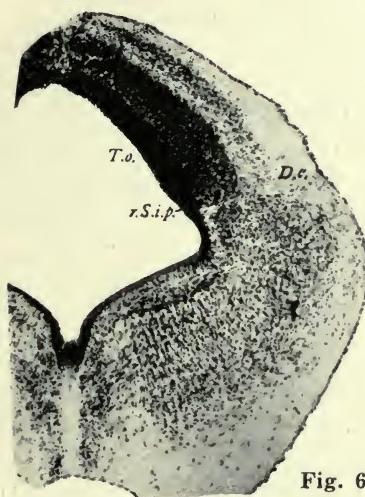


Fig. 61.

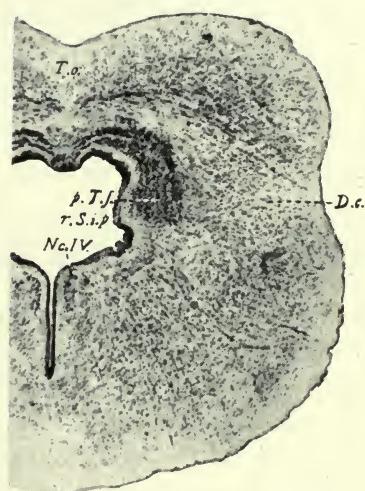


Fig. 62.

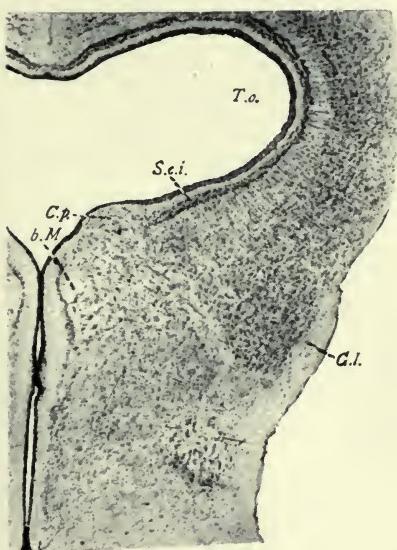


Fig. 63.

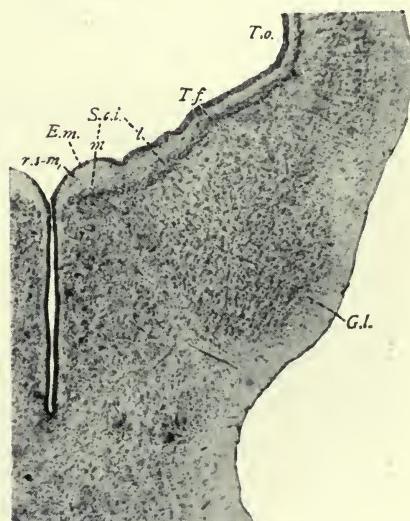


Fig. 64.

ventricle (*Torus semicircularis*). The cell-nucleus in question constitutes a direct continuation of the *Torus-formation* caudad. It finishes a little before the caudal medial part of the *Mesencephalon* dorsally to the *Fissura rhombo-mesencephalica*, i. e. is not connected caudally and medially with its *vis-à-vis* on the opposite side.

On sagittal sections of stages 8,0 and 15,0 cm. a part corresponding approximately in size to the dorsal *Subtectum* part, can be distinguished between the *Tectum-formation* and *Fissura rhombo-mesencephalica* (Figs. 40-98). In the *Stratum cellulare externum* of this part the cells lie more scattered and are less numerous than otherwise in the *Tectum*. This part constitutes the posterior and medial portion of the dorsal part of the *Subtectum*.

By using the above described structural features as points of vantage, it becomes easy to determine the *anterior boundary of the mid-brain* in its relation to the nuclei on the series of transverse sections.

In front of the *Eminentia medialis* of KAPPERS the *Stratum cellulare internum* (S. c. i. Fig. 63) is (up to stage 15,0 cm.) considerably broader in *Tectum* than in *Diencephalon* and stops suddenly immediately dorsal to (behind) the *Commissura posterior* fibres (C. p. Fig. 63), which like the blood-vessels, rows of cells and ependymal fibres run in a ventro-lateral direction towards the surface of the brain, and separate the "Geniculatum laterale" (G. l. Fig. 63) from the *Diencephalon*. At any rate up to stage 8,0 cm. this nucleus lies clearly dorsal to (behind) the boundary-plane, but appears later to be displaced in a ventral direction.

On sections lying directly caudad of the primary boundary-ridge (r. s—m<sub>1</sub> Fig. 64)<sup>1</sup> the thickened part of the *Stratum cellulare internum* in the medial part of the *Subtectum* begins to appear (S. c. i. m. Fig. 64). Dorsally to this part we find the foremost portion of the lateral part.

A few sections still further caudad, the *Torus-formation* (T. f. Fig. 64) appears, which thus does not extend quite to the boundary-plane. Peripherally

<sup>1</sup> This ridge which at stage 15,0 cm. partly remains on the ventral side, where it enters into the formation of the *Eminentia medialis*, is characteristically vacuolized and can therefore be easily recognized on transverse sections of the brain.

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Figs. 65 and 66. Transverse-sections through the anterior part of the mid-brain of *Acanthias* at stages 3,9 and 5,0 cm. (Microphotographs.) Fig. 67. Transverse-section through the *Torus lateralis* of *Salmo* at stage 0,9 cm. (sketch). Fig. 68. Transverse-section through the *Torus lateralis* of *Salmo* at stage 1,0 cm. (sketch). Fig. 69. Transverse-section of the *Torus lateralis* of *Salmo* at stage C. Fig. 70. Transverse-section through the *Torus lateralis* of *Salmo* at stage D. (Microphotographs.)

b. M., the bundle of Meynert; C. p., Commissura posterior; D. c., the dorsal part and column; G. l., Ganglion geniculatum laterale; L. c., the lateral part and column; S., Syncerebrum; S. c. i., m., the medial part of the *Stratum cellulare internum*; S. l. t., Sulcus lateralis tecti; T. l., Torus lateralis; I. 2. 3., the grooves in the region of the *Torus lateralis*; T. o., Tectum opticum.

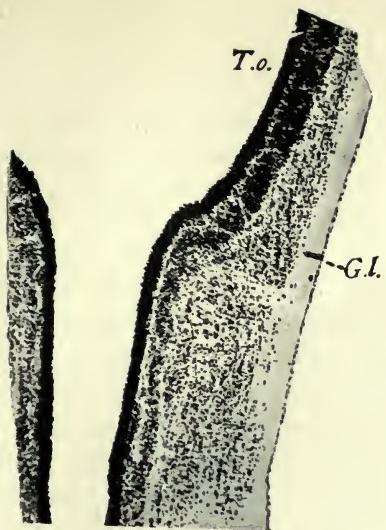


Fig. 65.

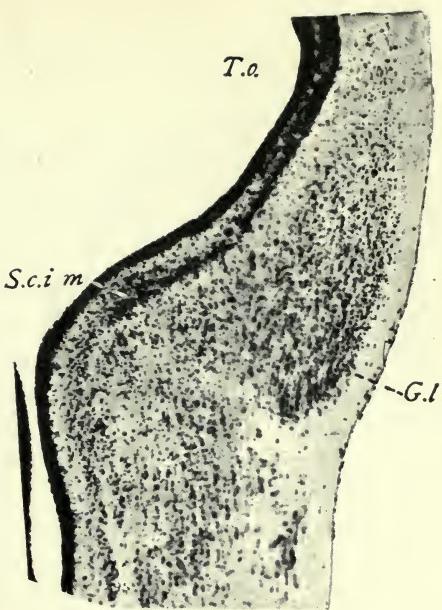


Fig. 66.

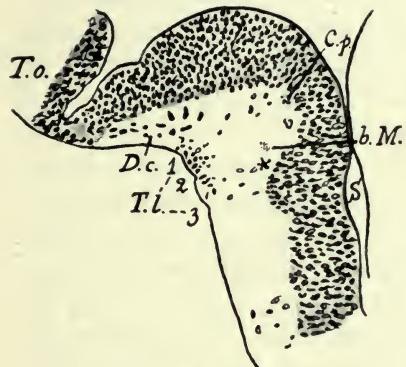


Fig. 67.

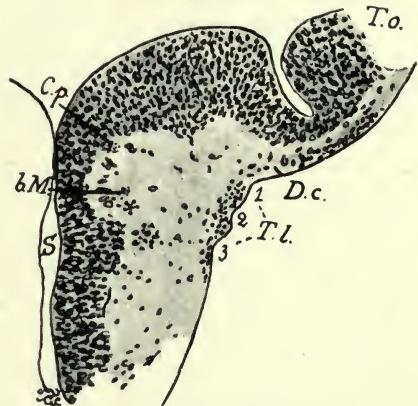


Fig. 68.



Fig. 69.

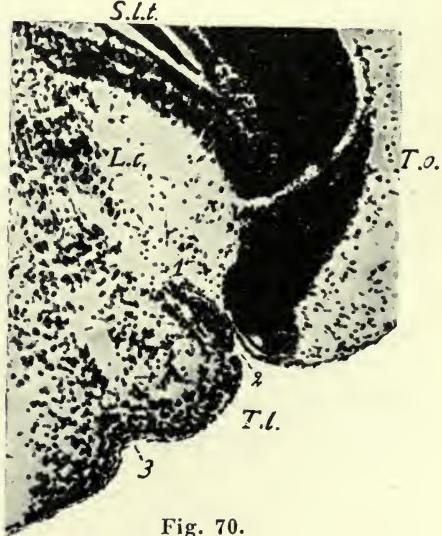


Fig. 70.

the "Geniculatum laterale" (G. 1. Fig. 64) is still visible, thus extending through three parts: the dorsal, the lateral and the medial. This nucleus is, in other words, a peripheric cell-mass in the anterior portions of those parts of whose Stratum cellulare internum it is formed (comp. Figs. 65, 66, 64).

The ventro-medial boundary-point is rather difficult to determine on transverse-sections. The bundle of MEYNERT is however a useful guide, lying ventro-medially in the boundary-plane, and so also is the Nervus III in accordance with what has been said above. It is evident that the ventral part of the Subtectum commences when the boundary-plane is passed.

The major part of the nucleus of the dorsal longitudinal bundle lies in the Synencephalon, but a few cells also protrude into the Mesencephalon.

### B. Teleostii (*Salmo salvelinus*).

Before passing on to a description of the embryonic development of the nuclei in *Salmo*, it would be as well to determine the position of the Torus lateralis in relation to the Fissura syn-mesencephalica and thereby to the segments. The question is therefore, is the Torus lateralis to be assigned to the Mesencephalon or to the Diencephalon?

KAPPERS (1907) describes the Torus lateralis in *Amia* as a ventral correspondence to the Torus semicircularis and consequently as a mesencephalic part of the brain. HOLMGREN (1920), on the contrary, accepts HALLER's interpretation, according to which the Torus lateralis is a diencephalic part detached from the Lobus lateralis hypothalami.

At stage 0,9 cm. of *Salmo salvelinus* it is possible to distinguish three grooves on transverse-sections through the region where the Torus lateralis is beginning to develop (Fig. 67). The central one is the Fissura syn-mesencephalica (2. Fig. 67) which is clearly developed ventrally and ventrolaterally (comp. above page 32 and Fig. 19 F. sm.). The nethermost groove (3. Fig. 67) is the one which on the medial sagittal section lies opposite the Tuberculum posterius (\* Figs. 19, 21). That this conception of the grooves is correct appears from a comparison between a series of sagittal and transverse-sections of this and earlier stages. The uppermost groove (1. Fig. 67) is not to be found at earlier stages, but appears first simultaneously with the peripheral cell-agglomeration, which at stage 0,9 cm. lies directly dorsal to the Fissura syn-mesencephalica (Fig. 67). This uppermost groove originates through the intumescence of the part in which this cell-agglomeration is found.

These three grooves (for the sake of brevity I call them 1, 2 and 3) are found again at later stages (at least up to stage D) and appear to be found also in full-grown *Osmerus*. At stage 0,9 cm. there lies as I have

said, in the region between grooves 1 and 2 a compact cell-agglomeration (Fig. 67). Between grooves 2 and 3 there are also some cells.

At stage 1.0 cm. (Fig. 68) the number of cells between grooves 2 and 3 has considerably increased and become fused with the cell-agglomeration between grooves 1 and 2 to a great peripheral cell-mass, which continues also in front of the part where the three grooves are found developed. The whole of this cell-mass (T. 1. Fig. 68) forms later the Torus lateralis.

At later stages the Torus-orientem increases and becomes more and more curved outwards. At stage C (Fig. 69) the caudal part of the Torus is divided up by the grooves into two nearly equal-sized parts. If the series of sections are followed in a forward direction the dorsal part is seen to diminish till it at last vanishes. Groove 2 does thus not run parallel with the Torus lateralis nor with groove 1, but converges frontad with this. Before the point where groove 2 stops Torus is undivided.

Finally at stage D (Fig. 70) groove 1 has, partly by the growth of the Tectum, partly of the Torus lateralis become singularly deep and sharply defined. Groove 2, on the contrary, is at this stage rather faint.

Groove 2 being the ventro-lateral part of the Fissura syn-mesencephalica, Torus lateralis or the caudal part of the same, is thus formed of a mesencephalic part which on transverse sections lies dorsal to this groove and to a ventro-diencephalic part.

I shall return to this later, for the present I will content myself with stating a fact, which seems to support this view.

In the full-grown *Osmerus eperlanus* Torus lateralis (T. 1. Figs. 76, 77) is divided up into two parts by a superficial, rather shallow groove (2 Figs. 76, 77), which is probably identical with the above described groove 2 (Fissura syn-mesencephalica) in *Salmo*. In *Osmerus* we find the point where grooves 1 and 2 converge is considerably further frontad, i. e. in the anterior part of the Torus lateralis.

Golgi and Haemalum preparations shew that specially vigorous ependymal-fibres issue from a point in the floor of the Tectum ventricle in a downward direction towards this groove (e. f. Fig. 76). Guided by the position of the boundary blood-vessel (b. v.) and of MEYNERT's bundle (b. M. Fig. 76), it can be determined with certainty that the point from which the ependymal-fibres issue, lies directly caudad of the boundary-plane between the Syn- and Mesencephalon. If these ependymal-fibres emanate radially which appears probable, the dorsal part of the Torus should be assigned to the mid-brain.

The form of the Mesencephalon in *Acanthias* differs very greatly from that in *Salmo*. An imaginary line drawn on a transverse section between the Sulcus longitudinalis ventralis and Sulcus lateralis tecti would in *Acanthias* run more or less vertically, in *Salmo*, on the contrary, already at

stage 0,6 cm. horizontally. The Tectum is, in other words, broader in *Salmo* and projects continually more downwards in a ventral direction, so that the Subtectum becomes more and more "exverted" (comp. Figs. 57, 71).

The *embryonic development of the nuclei* has been investigated chiefly at the following stages: 0,6, 0,7, 0,8, 0,9, 1,0, 1,1, 1,2 cm. and at stages C and D.

At stage 0,6 cm. a fibre layer outside the neuroblastic stratum is already to be found. In Tectum on the contrary, the neuroblastic stratum extends to the periphery. The boundary between the Tectum and Subtectum runs, as in *Acanthias*, immediately ventral to the widest part of the ventricle (Sulcus lateralis tecti).

Not till stage 0,8 does the development of the Stratum cellulare externum in Subtectum begin by cells wandering out into the fibre layer from that part of the neuroblastic stratum, which lies directly medial (ventral) to the boundary-line between the Tectum and Subtectum. A cell-column (D. c. Fig. 71) is thus formed, which in consequence of its position can be said to be homologous with the dorsal column of *Acanthias*. The wall of the Tectum has at this stage considerably thickened, this does however not refer to the caudal part of the mid-brain roof, where the wall is still comparatively thin.

At stage 0,9 cm. single cells begin to wander out from the more medial parts of the neuroblastic stratum in Subtectum towards the periphery, there to form a compact cell-agglomeration in the region where the Torus lateralis will develope (Fig. 67). In this manner is formed the oriment to the above mentioned dorso-caudal part of the Torus lateralis. No boundary exists between the Torus-oriment and the dorsal column<sup>1</sup>.

It is to be noticed, however, that the ventral part of the cell-agglomeration (dorso-caudal part of Torus) lies nearer the surface of the brain than does the dorsal column, which as in *Acanthias* lies approximately in the centre of the fibre layer.

The dorso-caudal part of the Torus-oriment is thus in continuity with the dorsal column and can be said to form a frontal major part of this latter. As the dorsal column in *Acanthias*, goes over frontad into a large cell-nucleus ("Geniculatum laterale"), which lies in, and is partly formed of the lateral and medial parts of the Stratum cellulare internum, we have not far to look for the "Geniculatum laterale" in *Acanthias* as homologous with the dorsal part of the Torus lateralis in *Salmo*. The homology rests on the following<sup>2</sup>:

<sup>1</sup> It is therefore possible although not probable that the entire cell-agglomeration of the periphery is formed from the dorsal part of the Subtectum through the dorsal column being tilted down in a ventral direction.

<sup>2</sup> Comp. KAPPERS and CARPENTER (1911): "Ich möchte hier auf der interessanten Tatsache hinweisen dass der von mir bei den Knochenganoiden: Amia und Lepidosteus, beschriebenen Torus lateralis vielleicht dem dorsalen Thalamus-Kern (the Geniculatum laterale) homolog ist." (P. 148.)

1) The dorsal cell-column is formed immediately ventral (medial) to the boundary between the Tectum and Subtectum, and lies in the fibre stratum outside the place where the Torus-formation is found (*Acanthias*) or will be formed (*Salmo*).

2) It extends further from the boundary-plane between the Mes- and Metencephalon frontad, where it passes into a large cell-agglomeration: "Geniculatum laterale" (*Acanthias*), the dorso-caudal part of the Torus lateralis (*Salmo*).

3) In both cases this nucleus is formed from the dorsal as well as the lateral and medial parts of the neuroblastic stratum, and

4) lies nearer the surface in both *Acanthias* and *Salmo* than does the dorsal column.

A cell-agglomeration is also to be found between grooves 2 and 3 at stage 1,0 cm. as appears from Fig. 68. This is the ventro-caudal part of the Torus lateralis. I cannot by reason of its position with certainty determine how this nucleus is formed, lying, as it does, close beside the dorsal mesencephalic part. It may therefore possibly be formed of cells which protrude in a ventral direction from this dorsal part. But there is also another possibility, which I consider more probable, namely that the ventral part of the Torus lateralis, which is, as mentioned, in the Synencephalon, is formed of cells migrating from the point \* Figs. 67, 68. Cells migrate from this point already at stage 0,9 cm. (Fig. 67) when the ventral part of Torus begins to develop, i. e. from those parts of the neuroblastic layer, which lie ventral (on transverse sections) to the Commissura posterior (C. p. Figs. 67, 68) and about the bundle of MEYNERT (b. M.) (thus in the Synencephalon) towards the periphery or ventral part of the Torus<sup>1</sup>.

At stage 1,0 cm. (Fig. 68) the cell-agglomerations forming the oriment of Torus lateralis has become still more elongated in a ventral direction. If the structural features received at stages 0,9 and 1,0 cm. are to be interpreted as proving that the ventral part of the Torus lateralis is formed of the dorsal part, it should, in consequence and by the same right be assumed that the cell-agglomeration, lying ventrally to the Torus is of mesencephalic origin. This cell-agglomeration continues caudal, however, into the hypothalamic region. I for my part, consider the formation of this nucleus (Nucleus diffusus lobi lateralis) from the mid-brain very improbable, even if the continuity of these cell-agglomerations make such a theory possible.

The migration of cells in the Subtectum has at stage 1,1 cm. advanced so far, that it has become possible to distinguish veritable columns in the

<sup>1</sup> This migration of cells should not be mistaken for that, which at stage 1,0 cm. begins to appear from a point lying somewhat more ventrally and is the origin of the Nucleus anterior thalami (according to as yet unpublished investigations by G. LINDÉN on the embryonic development of the nuclei in *Salmo*).

lateral and medial parts of the Subtectum. The Stratum cellulare internum is approximately in the centre of the Subtectum, somewhat thickened and forming a pointed projection into the fibre layer (Fig. 72). A column (L. c. Fig. 72), relatively rich in cells, has developed from this point, which for reasons given below, has been pronounced homologous with the lateral column of *Acanthias*. More scattered cells lie medial to this column, radiating from the region round and lateral to the Fasciculus longitudinalis dorsalis. I consider these cells (M. c. Fig. 72) to correspond with the medial column of *Acanthias*.

A peripheral cell-group (p. c. Fig. 72) lies at this stage caudad to the Torus lateralis region, and extends from the tectum-subtectum boundary in a medial direction over both the lateral and medial parts. The cells in this group are somewhat less numerous laterally i. e. in the dorsal part, but I can discover no boundary between the dorsal column and the rest of the part. Peripheral cell-nuclei are to be found, as above mentioned, in the lateral part of *Acanthias*, where the nucleus is comparatively distinct, as in the medial, where, however it is only possible to speak of a defined cell-condensation at certain stages. I consider probable that in *Salmo* parts homologous to these nuclei form part of the peripheral cell-group. The position and, as far as it is possible to judge, the embryonic development of these parts point to this.

The medial parts of the peripheral cellnucleus are also in continuity with the oriment of the dorsal part of the Torus lateralis. A compact cell-mantle of, as I believe, heterogeneous origin, thus lies at the whole of the ventro-lateral surface of the Subtectum.

*At stages 1,2 cm. and C*, the columns are richer in cells, and at the same time more clearly defined than at previous stages.

*At stage D* (Fig. 73) a compact small-celled cell-column is found ventral to the Nucleus III in the ventral part of the Subtectum. There is a density of cells (Nucleus ruber?) under the Fasciculus longitudinalis dorsalis i. e. in the lateral portion of the ventral part. Lateral to the Fasciculus longitu-

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Figs. 71—73. Transverse-sections through the mid-brain of *Salmo* at stages 0,8 and 1,1 cm. and stage D. Fig. 74, Transverse-section through the mid-brain of *Lepidosteus*. Fig. 75. Transverse-section through the mid-brain of *Rana* at stage 3,6 cm. (Micro-photographs.)

D. c., the dorsal column; F. l. d., Fasciculus longitudinalis dorsalis; H, the hypothalamic region; L. c., the lateral column; M. c., the medial column; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; N. l. m., Nucleus lateralis mesencephali; p. c., the peripheral cell-mantle; S. c. i., m., l., the medial and lateral parts of the Stratum cellulare internum; S. l. t., Sulcus lateralis tecti; S. l. v. Sulcus longitudinalis ventralis; St, Subtectum; T. f., the Torus-formation; T. l., Torus lateralis; T. o., Tectum opticum; T. s., Torus semicircularis; V. c., the ventral column; Vl. c., Valvula cerebelli.

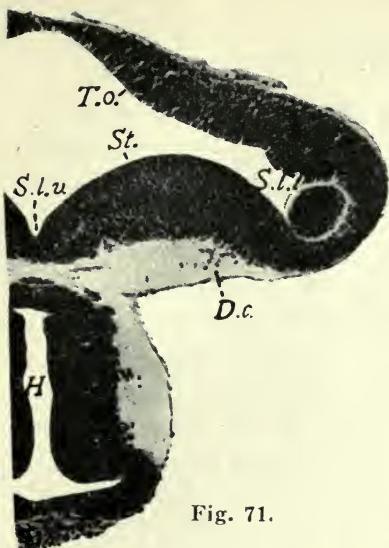


Fig. 71.

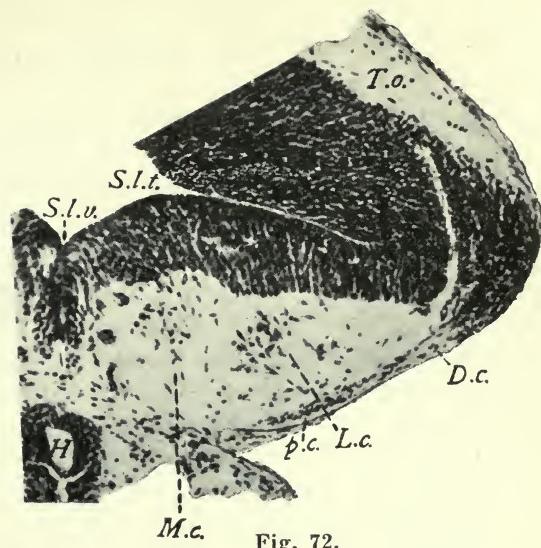


Fig. 72.

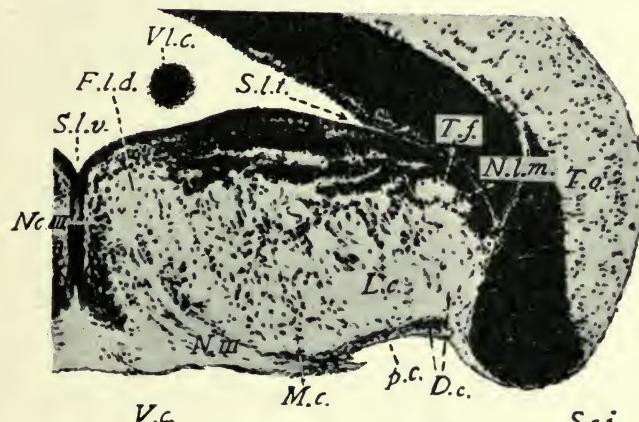


Fig. 73.

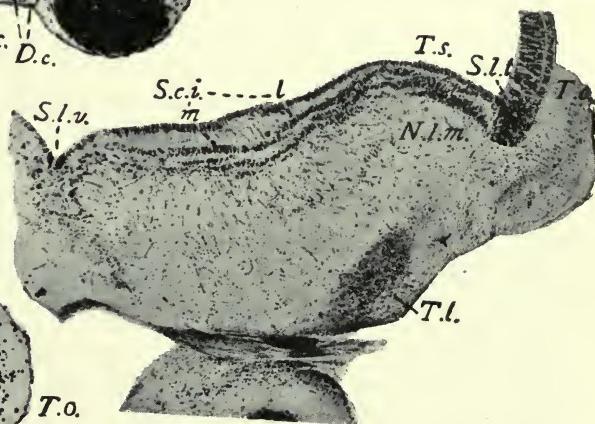


Fig. 74.

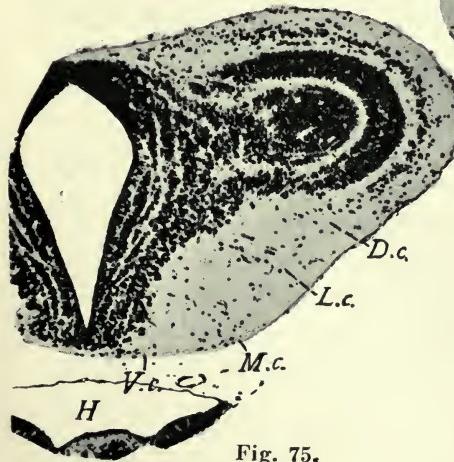


Fig. 75.

dinalis dorsalis there is to be found in *Salmo* at this and earlier stages, as above mentioned, two fairly distinct columns: the medial and the lateral.

In *Salmo* the structural features: Sulcus lateralis and the differentiation of the Stratum cellulare internum, used in *Acanthias* for determining the boundary between the medial and lateral parts, are indeed lacking; in *Lepidosteus*, on the contrary, the medial part of the Stratum cellulare internum (S. c. i. m. Fig. 74) is composed of comparatively closely packed cells. It seems probable that this part corresponds with the medial thickened portion of the same cell-layer in *Acanthias* (S. c. i. m. Fig. 59). If this be correct, the difference between the topographical positions of the various parts in *Lepidosteus* and *Salmo* not being great, it may be considered that the medial of the two above mentioned columns in *Salmo* is homologous with the medial column in *Acanthias*, and the lateral one with the lateral column of *Acanthias*. It should be noticed that a number of comparatively large cells are to be found in the medial part and close to the ventricle in both *Osmerus* (Fig. 77) and *Labrus*. These cells do not however form any true cell-layer (Stratum cellulare internum).

The metencephalic columns, which in *Salmo* as in the other animal types, are better defined than the mesencephalic columns, form a direct continuation of these latter, a fact which also points to a correct designation of the columns in *Salmo*.

*Salmo* is an unsuitable subject for a study of the embryonic development of the Nucleus ruber. The Nucleus ruber of GOLDSTEIN (1905) is very indistinctly developed in this species as in *Osmerus*, but in *Labrus*, on the contrary it is well-defined, though lying in quite the foremost part of the medial column on the boundary to the lateral. As the Nucleus ruber in *Gallus* and *Mus* is a differentiation in the ventral column, the Nucleus ruber of GOLDSTEIN can hardly be said to be homologous with the Nucleus ruber in Amniotes. HOLMGREN (1920) has come to the same conclusion, he writes: "Die gekreuzten Bindearme des Cerebellums haben, soweit es aus hunderten von Schnittserien hervorgeht, bei *Osmerus* keine intimeren Verbindungen mit dem Kern, der somit schwerlich mit dem Nucleus ruber der höheren Vertebraten homolog sein kann. Die Bindearme durchsetzen den Kern" (page 145).

The Stratum cellulare internum of the dorsal part is, at stage D in *Salmo*, hollowed out in a semicircular form and consists of only one unified layer of cells nearest to the tectum-subtectum boundary (T. f. Fig. 73). This semicircular part of the Stratum cellulare internum corresponds in position and appearance with the Torus-formation in *Acanthias*. This Torus-formation constitutes the major part of the Torus semicircularis in full-grown teleosts.

Cells migrate from the Stratum cellulare internum in the caudal portion of the lateral part in a ventral and somewhat lateral direction till they occupy a position in the Torus semicircularis. A few cells are to be found in the

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Torus-formation proper already at stage D (N. l. m. Fig. 73). These become more numerous later and form the Nucleus lateralis mesencephali.

The above mentioned cell-mantle (p. c. Figs. 72, 73), becomes more and more reduced and finally disappears completely. In *Osmerus*, however, a small part of the same remains dorsal to the caudal part of the Torus lateralis and lateral to the optic tract, even in the fully developed brain. This nucleus (\* Fig. 77) is in continuity frontad with the dorsal part of the Torus lateralis.

The Torus lateralis proper has, in *Lepidosteus*, a caudal, undoubtedly mesencephalic part (T. l. Fig. 74), which extends about as far caudad as the Torus semicircularis (Fig. III). It appears to me conceivable that it is this caudal part which KAPPERS (1907) refers to when he says that the Torus lateralis in *Amia*: "als ein extraventricularer Auswuchs, man könnte sagen exvertierter Teil desselben (Torus semicircularis), angesehen werden könnte" (page 470).

The Corpus geniculatum laterale in Teleosts is formed, according to LINDÉN<sup>1</sup>, by cell-migration from a frontal part of the mesencephalic neuroblastic layer. The point at which the Geniculatum is formed, lies partly anterior, partly dorsal to the point at which "Geniculatum laterale" is formed in *Acanthias*. Geniculatum in *Salmo* is found primarily in the Tectum, in *Acanthias* in the Subtectum. Moreover, as Geniculatum in *Salmo* has not the slightest connection with the dorsal column, the nucleus, which in *Acanthias* is designated Geniculatum laterale cannot be homologous with Geniculatum laterale in the Teleosts. I have not been able to discover a differentiated nucleus answering to the latter in *Acanthias*. In *Chimaera*, on the contrary, there is, according to KAPPERS AND CARPENTER (1911), a typical Geniculatum laterale frontad of and separated from a larger nucleus (Nucleus dorsalis thalami), which clearly is the same as "Geniculatum laterale" (Geniculatum mediale of WALLENBERG) in *Acanthias*.

Finally, I am in complete agreement with HOLMGREN (1920) regarding Nucleus corticalis, when he says that this nucleus should be assigned to the Tectum-opticum. It is undoubtedly formed from Tectum parts of the neuroblastic layer.

### C. Amphibia (*Rana temporaria*).

The development of the nuclei begins comparatively late in *Rana*. Not till the larva shews well-defined oriments of caudal extremities, is the cell-migration from the neuroblastic layer at all distinct. At stage 3,6 cm. the differentiation of the nuclei is in the main concluded. In the ventral part

<sup>1</sup> The studies on the embryological development of the nuclei in *Salmo* by G. LINDÉN are not yet published.

(V. c. Fig. 75) there is at this stage only a small number of cells in the fibre stratum ventral to the Nucleus III. This latter nucleus is, however, not clearly differentiated till after the larval stages are concluded.

In the fibre-layer of the medial part (M. c. Fig. 75) the cells are comparatively few in number. The nucleus described by GAUPP (1899) as Nucleus ectomammillaris is found, at earlier stages, frontad of the boundary-plane between the Syn- and Mesencephalon. A peripheral cell-group is, at later stages, formed from the medial column. This cell-group is in continuity with the diencephalic part of the Nucleus ectomammillaris.

The lateral column (L. c. Fig. 75) is fairly rich in cells, and is formed from a projecting part of the neuroblastic layer, which strongly resembles the part from which the lateral column in *Salmo* is formed.

Outside the Torus-formation, we find a number of cells in the fibre-layer, a dorsal column (D. c. Fig. 75) continuous with the Stratum cellulare externum in the Tectum, but distinguishable from the Tectum layer by the greater compactness of the latter. I cannot discover in *Rana* any frontal part of this column corresponding to the "Geniculatum laterale" in *Acanthias*. We also find diffusely distributed cells, which form the Nucleus lateralis mesencephali, in the Torus-formation itself. By the term Torus-formation I define the semicircular part of the Stratum cellulare internum. The hemispherical elevation in the floor of the mid-brain (Torus semicircularis), does not coincide completely with the Torus-formation. The lateral part with its column will be found within the Torus semicircularis ventral to the Torus-formation proper.

I have, by reason of the lack of material, not been able to investigate the embryonic development of the nuclei in Reptiles.

#### D. Aves (*Gallus domesticus*).

The development of the nuclei in *Gallus* has been investigated at the following stages: 6, 7, 8, 8½, 9, 10 and 15 days.

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Figs. 76, 77. Transverse-sections (of the same series) through the mid-brain of *Osmerus*. Fig. 78. Transverse-section through the mid-brain of *Gallus* at the 6 day stage. (Microphotographs.)

b. M., the bundle of Meynert; b. v., the "boundary-vessel"; D. c., the dorsal part; e. f., ependymal fibres; F. l. d., Fasciculus longitudinalis dorsalis; L. c., the lateral part; M. c., the medial part; m., l., the medial, lateral portion of the part in question; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; N. l. m., Nucleus lateralis mesencephali; O. t., the optic tract; S. l., Sulcus lateralis; S. l. v., Sulcus longitudinalis ventralis; T. l., Torus lateralis; 1, 2, 3, the three grooves in the region of the Torus lateralis; T. s., Torus semicircularis; T. o., Tectum opticum; V. c., the ventral part; vl., the ventro-lateral portion of the ventral part; VI. c., Valvula cerebelli.

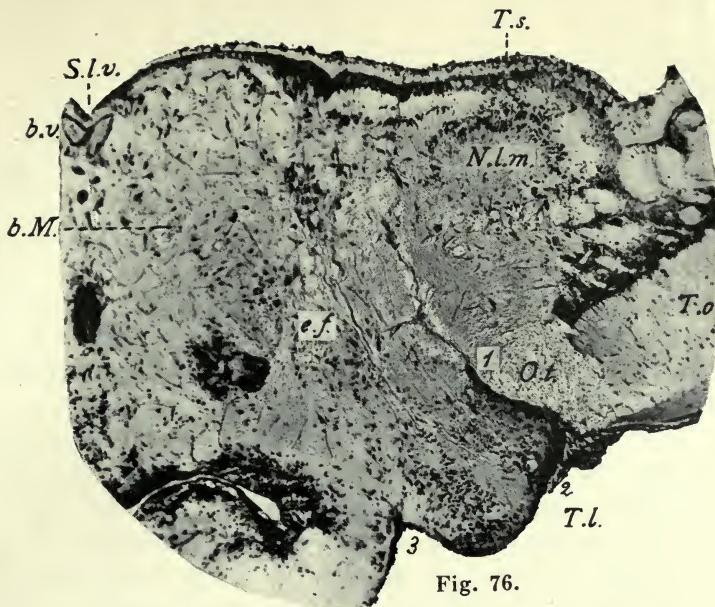


Fig. 76.

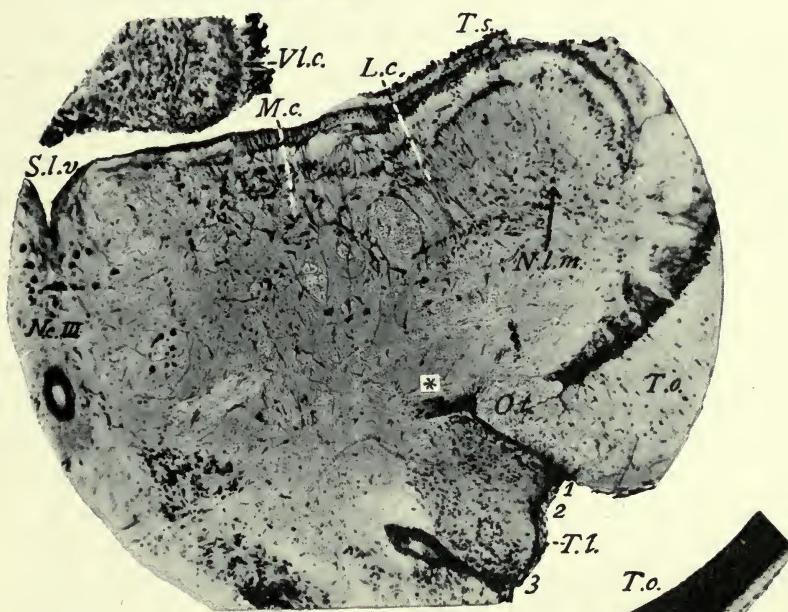


Fig. 77.

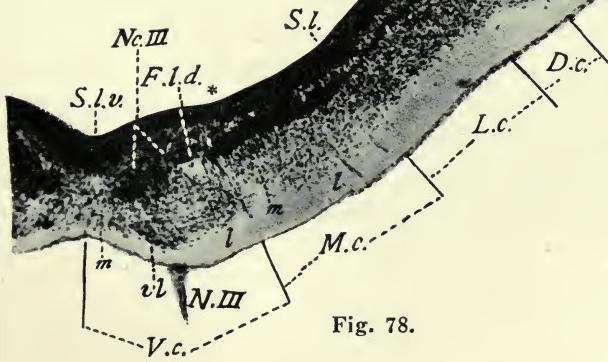


Fig. 78.

The 6 day stage (Fig. 78). The wall of the Tectum consists at this stage of a compact neuroblastic layer and outside that, a thin fibre-layer. Three cell-layers have, on the other hand, developed in the Subtectum: Stratum ependymale, Stratum cellulare internum and Stratum cellulare externum.

Lateral to the Sulcus longitudinalis ventralis (S. l. v. Fig. 78), we find in Subtectum two longitudinal ventricular grooves, of which the medial (\* Fig. 78) lies directly lateral to the Fasciculus longitudinalis dorsalis and bounds the "Haubenwulst" on the lateral side. The lateral groove is Sulcus lateralis (S. l. Fig. 78).

Different parts can be distinguished in the Stratum cellulare internum according to the compactness or paucity of cells in the layer. As these parts are in conformity with the corresponding parts in *Acanthias*, the same subdivision of the Subtectum can be carried out in *Gallus*.

In the ventral part, which can be delimited in the same way as in *Acanthias*, and also by means of the above mentioned ventricular groove at the side of the "Haubenwulst" (\* Fig. 78), the Stratum cellulare internum is considerably thickened, but is not, as in *Acanthias*, thinner dorsal to the Fasciculus longitudinalis dorsalis. The cells composing this layer are comparatively large and form the oriment of the Nucleus III. A ventral cell-column differentiated as follows, is found in the fibre-layer: A number of lesser cells lie close to the medial line; ventro-laterally the cells form a peripheral cell-group (vl. Fig. 78). The cells in this group are fusiform, as in *Acanthias*, and arranged with their longitudinal axes in a lateral direction. As neuroblasts are generally bi-polar and arranged with their longitudinal axes in the direction of migration, it might be supposed that the arrangement of the cells in this peripheral cell-group was a proof of their being in the act of migrating in a lateral direction. This does not however, seem to be the case. At stage 6 days the lateral part of the cell-agglomeration in question lies slightly lateral to the Nervus III. In the same position it is also to be found at later stages, still with the characteristic cell-arrangement.

Outside the Fasciculus longitudinalis dorsalis lies a cell-agglomeration (V. c., l. Fig. 78), to which there is a correspondance in *Acanthias*. In *Acanthias* these cells are formed from the part of the Stratum cellulare internum surrounding the Fasciculus longitudinalis dorsalis (stage 3,9 cm. [Fig. 57]). At the 6 day stage this nucleus is, in *Gallus*, connected with neuroblasts migrating from the corresponding point, but it is also in continuity with laterally directed bi-polar cells in more medial parts of the ventral column. In *Acanthias* (at e. g. stage 5,0 cm.) the cells are arranged in the same way in the corresponding part of the ventral column. It can be left an open question, however, whether a true cell-migration takes place in a lateral direction from the medial part of the ventral column, or not.

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The Stratum cellulare internum is likewise thickened between the Sulcus lateralis and the "Haubenwulst", but consists of comparatively small cells. There are only a tolerably few scattered cells in the fibre-layer of this medial part (M. c. Fig. 78), comp. *Acanthias*, stage 3.9 cm. (Fig. 57). The cell-migration from the medial portion of the Stratum cellulare internum (M. c., m. Fig. 78) appears to be somewhat more vigorous than in the lateral (M. c., l. Fig. 78). The cell-density is somewhat greater medially than laterally in the medial part (M. c. Fig. 78).

The Stratum cellulare internum is comparatively thin at that part of the Subtectum which lies dorsal to the Sulcus lateralis (S. l. Fig. 78), but becomes thicker towards the Tectum. The Stratum cellulare externum is composed of a compact mass of cells, which however becomes more sparse dorsally. Thus it is already possible at this stage to detect a differentiation into two parts, a dorsal (D. c. Fig. 78) and a lateral (L. c. Fig. 78).

The 7 day stage (Fig. 79). The lateral part of the ventral column (lying under the Fasciculus longitudinalis dorsalis) has increased in size, so that a larger unified nucleus (\* Fig. 79) has formed, in which practically all the cells are fusiform and horizontally disposed. This nucleus has also enlarged in a lateral direction and is now found partly in the medial part, that is to say, the boundary between the ventral and medial parts has, by reason of the increase of cells, disappeared. However, the boundary-line between the ventral column and the medial is evidently immediately median of a condensation in the lateral portion of the cell-group \* Fig. 79, though it cannot be discerned in the Stratum cellulare externum.

No important change has taken place in the medial part. In the lateral part the Stratum cellulare internum has entirely vanished. In the dorsal part the oriment of the Torus-formation can henceforth be clearly distinguished.

The Stratum ependymale has become thicker, partly under the Sulcus longitudinalis ventralis (as at the previous stages), partly at Sulcus lateralis.

The 8 day stage (Fig. 80). By reason of the increase of cells in the Stratum cellulare externum, the boundaries between the different columns have at this stage become rather difficult to discern. The same parts in the Stratum cellulare internum can however be observed as at the preceding stages. The thickening of the Stratum ependymale at the Sulcus lateralis can likewise still be used as a point of vantage, but the groove has almost been eliminated.

Ventral to the Fasciculus longitudinalis dorsalis a cell-condensation is found, which corresponds to the medial portion (belonging to the ventral column) of the cell-group \* Fig. 79. The cells of this portion are somewhat larger than in the rest of the column. These cells form a nucleus, which becomes still more distinct later: Nucleus ruber.

The structure of the ventral part is otherwise in the main the same as at the preceeding stages.

In the medial part the Stratum cellulare internum is not so compact as at the preceeding stage, but is instead broader (S. c. i. m. Fig. 80). The number of cells is less in the lateral (M. c., l. Fig. 80) than in the medial portion (M. c., m. Fig. 80) of the medial column. The Stratum cellulare internum is lacking in the lateral part as at the 7 day and following stages. A lateral column or condensation in the Stratum cellulare externum can be observed (L. c. Fig. 80).

The Torus-formation (T. f. Fig. 80) is more distinct than at the 7 day stage, and is composed of a differentiated part of the Stratum cellulare internum. A compact neuropil-substance has namely developed in this layer, surrounded by closely-packed cells, which are seen disposed in a semicircle on transverse-sections. The cells in the Neuropilema (Nucleus lateralis mesencephali) do not lie so closely-packed as is otherwise the case in the Stratum cellulare internum. Outside the Torus-formation (between it and the optic tract [O. t. Fig. 80]) lie a number of cells (D. c. Fig. 80), which, later (stage 15 days), form a distinct nucleus. This nucleus lies in the same position as the dorsal column in *Acanthias*, but does not get merged frontad in any larger nucleus. I cannot discover in *Gallus* any equivalent to the "Geniculatum laterale" in *Acanthias*.

A number of scattered cells are already visible at the 8 day stage in the periphery of the medial part, these cells have become more numerous at the  $8\frac{1}{2}$  day stage, and form a distinct peripheral nucleus in this part. This is the oriment of the Ganglion opticum basale (Ganglion ectomammillare) (EDINGER).

The 9 day stage (Fig. 81). At this stage the Nucleus ruber (Nc. r.) like the Nucleus ectomammillaris can clearly be distinguished. The compact-cellulated mantle in the Torus-formation has almost disappeared, there remains on the other hand, the comparatively dark-coloured neuropil-substance with the Nucleus lateralis mesencephali.

The 10 day stage (Fig. 82). The most striking change which has taken place at this stage, is the vigorous growth of the Torus semicircularis

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Figs. 79—81. Transverse-sections through the mid-brain of *Gallus* at the stages 7, 8 and 9 days. (Michrophotographs.)

D. c., the dorsal part and column; F. l. d., Fasciculus longitudinalis dorsalis; L. c., the lateral part and column; M. c., the medial part and column; m., l., the medial, lateral portion of the part in question; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; Nc. e., Nucleus ectomammillaris; Nc. r., Nucleus ruber; O. t., the optic tract; S. c. i. m. l., the medial, lateral part of the Stratum cellulare internum; S. l., Sulcus lateralis; S. l. v., Sulcus longitudinalis ventralis; T. f., the Torus-formation; T. s., Torus semicircularis; T. o., Tectum opticum; V. c., the ventral part and column; v.l., the ventro-lateral portion of the ventral column.

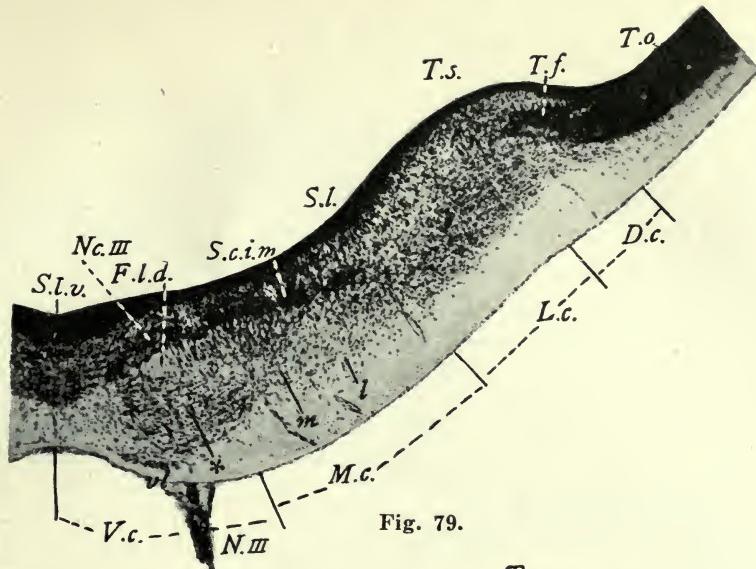


Fig. 79.

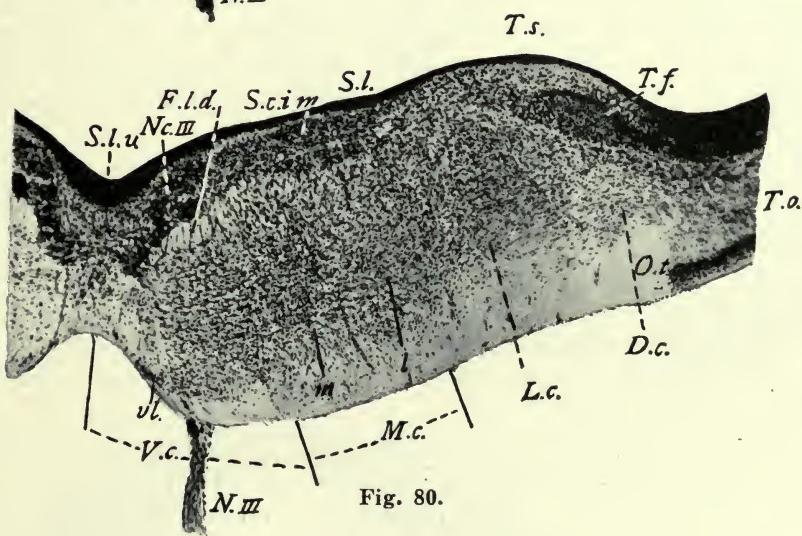


Fig. 80.

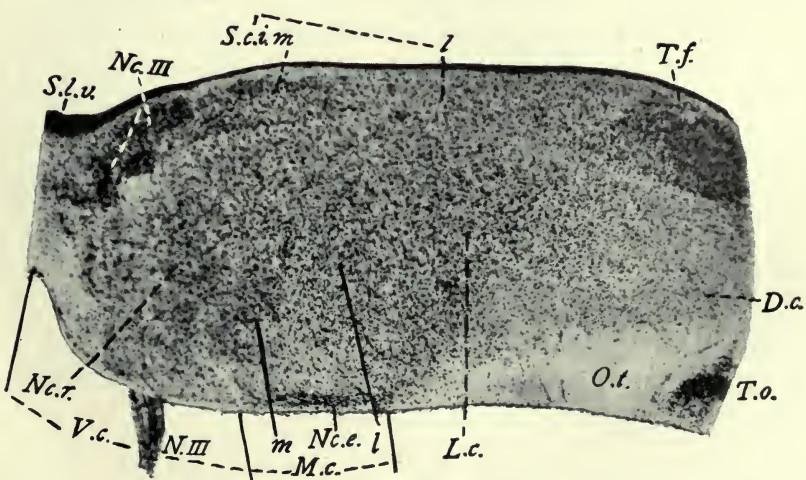


Fig. 81.

(T. s. Fig. 82). The Torus semicircularis appears, on transverse-sections, as a semilunar part sharply projecting into the ventricle. It is quite clear that the Torus semicircularis is composed of the lateral part as well as of the Torus-formation proper (comp. Figs. 79, 80, 82). The ventral boundary of the Torus semicircularis coincides with the boundary between the medial and lateral parts. The lateral (dorsal) portion only of the Torus semicircularis is filled by the Torus-formation (T. f. Fig. 82), such as it has developed into since its first appearance in the Stratum cellulare internum.

The 15 day stage (Fig. 83). In the ventral part (V. c. Fig. 83) we find the now very well-defined Nuclei III (Nc. III Fig. 83) and the Nucleus ruber (Nc. r. Fig. 83), which is composed of similar, although not so tightly-packed cells. The rest of the ventral column consists of a mass of very small cells. The above-mentioned ventro-medial portion (vl. Figs. 78, 79, 80) can no longer be distinguished. (It vanishes more and more during the 8½—10 day stages). The cell-group m. Figs. 80—83 (the Ganglion profundum mediale of EDINGER) remains. Ganglion opticum basale lies here peripherally and the remainder of the section is filled with a diffuse mass of cells.

In the Torus semicircularis, medial to the Torus-formation, and therefore in the lateral part, we find a fairly compact cell-mass, indications of which are already noticed at preceding stages. In the centre of the lateral part we also find a cell-condensation (the Ganglion profundum laterale of EDINGER).

The Torus-formation proper or Nucleus lateralis mesencephali (T. f. Fig. 83) continues to occupy only the lateral portion of the Torus semicircularis.

Medial to the dorsal column there is at this stage another well-defined nucleus (Nc. i. Fig. 83), whose embryological development points to its being correctly assigned to the Metencephalon, i. e. the Isthmus region. Lateral to the Velum medullare anterius, dorsal to the lateral groove in the 4<sup>th</sup> ventricle, and caudal to the boundary-plane between Mes- and Metencephalon (therefore in the Isthmus) a nucleus, Ganglion isthmi, is to be

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Figs. 82, 83. Transverse-sections through the mid-brain of *Gallus* at stages 10 and 15 days. Fig. 84. Transverse-section through the mid-brain of *Mus* at stage 0,8 cm. (Microphotographs.)

D. c., the dorsal part and column; F. l. d., Fasciculus longitudinalis dorsalis; L. c., the lateral part and column; M. c., the medial part and column; m., l., the medial, lateral portion of the part in question; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; Nc. e., Nucleus ectomammillaris; Nc. i., the frontal part of the Nucleus isthmi; Nc. r., Nucleus ruber; O. t., the optic tract; S. c. i., m., the medial part of the Stratum cellulare internum; S. l., Sulcus lateralis; S. l. v., Sulcus longitudinalis ventralis; T. f., the Torus-formation; T. o., Tectum opticum; T. s. Torus semicircularis.

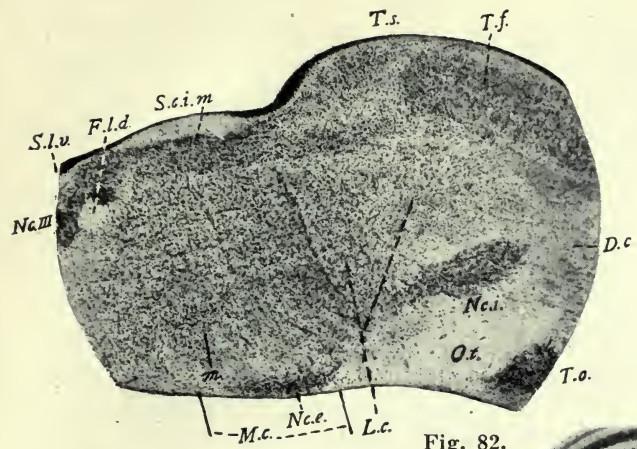


Fig. 82.

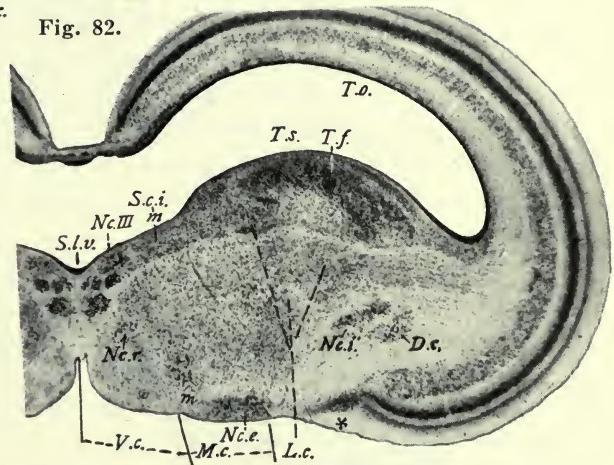


Fig. 83.

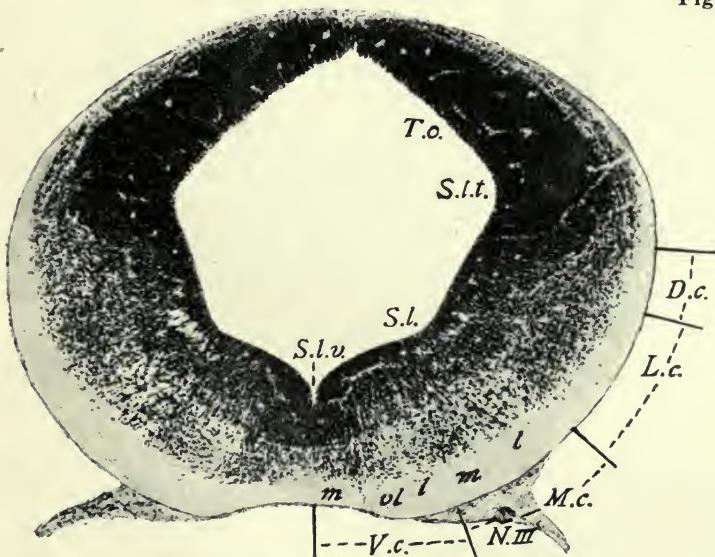


Fig. 84.

found in *Acanthias*. At the 6 day stage of *Gallus*, a singularly well-defined and compactly cellulated nucleus lies in the same position as the Ganglion isthmi occupies in *Acanthias*. The lateral and frontal part of this nucleus increases in size so much that at the later stages it projects continually more frontad and finally crosses the boundary of the Mesencephalon and takes up its position medial to the dorsal column at the 15 day stage. That this nucleus should properly be assigned to the Isthmus region, that is to say, that it is formed by the growth of the frontal and lateral parts of the Ganglion isthmi (Nc. i. Fig. 99), I therefore consider proved by the following facts: 1) that it has exactly the same very characteristic structure at the 6—10 day stages as Ganglion isthmi, and is in continuity caudad with this nucleus, 2) that its growth can be followed step by step during its embryonic development.

Thus I completely agree with BELLONCI (1888), when he says: "Beim Huhn ist er (Corpus posterius, Nucleus isthmi) schon am 10. Tage der Bebrütung deutlich zu sehen und senkt sich unter allmählicher Größenzunahme in die eigentliche Substanz des Lobus opticus ein" (p. 29). Under the name of Nidulus sub-pyriformis TURNER (1891) describes this nucleus as belonging to the mid-brain.

I have been unable to discover any analogy to the cell-nucleus \* Fig. 83 so clearly developed in the anterior part of the mid-brain and in the optic tract at the 15 day stage among the remaining animal species investigated by me.

The nucleus in question is not yet developed at the 10 day stage; it develops therefore comparatively late. It can hardly be considered homologous with the dorsal column, partly by reason of its lying, as above mentioned, wedged right into the optic tract, partly because it develops only in the anterior part of the Mesencephalon. The dorsal column is found, as I have said, also in the caudal portion and extends towards the Velum region.

Neither can this nucleus be compared with the "Geniculatum laterale" in *Acanthias*, as no proof can be given of any connection between it and the dorsal column. In addition to this, the "Geniculatum laterale" develops already very early and in a different position in relation to the optic tract.

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Figs. 85, 86. Transverse-sections through the mid-brain of *Mus* at stages 1,0 and 1,3 cm. (Microphotographs.)

D. c., the dorsal part; L. c., the lateral part; m., l., the medial, lateral portion of the part in question; M. c., the medial part; N. III, Nervus oculomotorius; Nc. III, Nucleus oculomotorius; Nc. r., Nucleus ruber; S. l. t., Sulcus lateralis tecti; S. n., Substantia nigra; S. l. v., Sulcus longitudinalis ventralis; T. o., Tectum opticum; V. c., the ventral part; vl., the ventro-lateral portion of the ventral column.

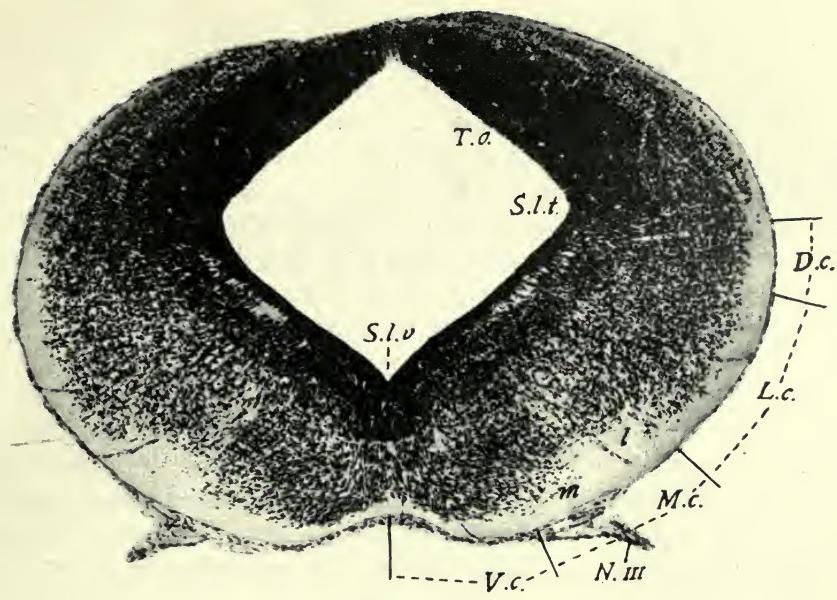


Fig. 85.

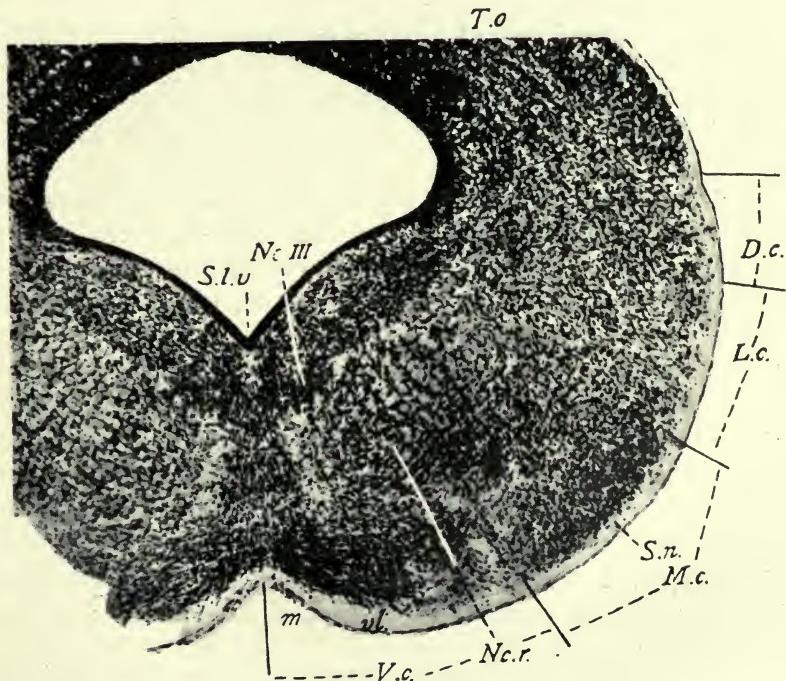


Fig. 86.

E. Mammalia (*Mus musculus* var. *albino*).

I have examined *Mus musculus* var. *albino* at stages: 0,8, 1,0, 1,3, 1,6, 1,9, 2,3 cm., young animals of 4,0 and 4,5 cm. in length, and the brains of full-grown white mice.

A study of the embryonic development of the nuclei in mammals offers considerable difficulty. The reason of this is, that the abundance of cells in the brain of mammals already at comparatively early embryonic stages, is so considerable, that it is not easy to draw up boundaries between the different parts.

At stage 0,8 cm. (Fig. 84), where the number of cells is not yet too great, the Subtectum can however be divided into parts in the same manner as e. g. in *Acanthias* and *Gallus*. The Stratum cellulare internum is not, to be sure, as in those species, divided up into broader and thinner parts, but on the other hand, the Sulcus longitudinalis ventralis (S. l. v. Fig. 84) and the Sulcus lateralis (S. l. Fig. 84) are very well-defined, and the disposition of the cells in Stratum cellulare externum is, broadly speaking the same as in *Acanthias* (Fig. 57) and *Gallus* (Fig. 78) at earlier stages (3,9 cm. and 6 days respectively).

In the ventral part (V. c. Fig. 84), the cell-mass in the fibre-layer (the ventral column) is composed of a medial part (m.) and a lateral (l.), which is situated ventrally to the Fasciculus longitudinalis dorsalis. Between these two parts in both of which there is a paucity of cells, the cells lie more closely-packed and are partly horizontally disposed (vl.) as in *Gallus* (comp. Fig. 78, vl.).

In the medial part can be distinguished in Stratum cellulare externum a medial portion (M. c., m. Fig. 84) with closely packed cells passing without any sharp boundary into the lateral portion of the ventral column (V. c., l. Fig. 84), and a lateral portion (M. c., l. Fig. 84) consisting of rather larger and not so closely packed cells.

A dense cell-mass, somewhat more closely packed ventrally, forms the lateral column (L. c. Fig. 84), lying in the fibre-layer dorsal to the Sulcus lateralis or the boundary-line between the medial and lateral parts. Dorsally the cellular mass passes continuously into the corresponding Tectum layer.

The boundary between the Tectum and Subtectum, namely the dorsal part, can at any rate approximately be determined firstly because the Sulcus lateralis tecti (S. l. t. Fig. 84) is clearly developed and secondly because the Stratum cellulare internum in Tectum is considerably more vigorous than in Subtectum.

*Stage 1,0 cm.* (Fig. 85). The medial, more abundantly cellulated part of the medial column (M. c., m. Fig. 85) has by the increase in the number

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of cells, become merged, together with the lateral part of the ventral column, into a large, fairly compact cellular mass.

Ventrally in the ventral part (V. c. Fig. 85) a dense cell-group can be distinguished: the ventro-lateral portion of the ventral column.

As the Sulcus lateralis is at this stage almost effaced, the boundary between the medial and lateral parts can only be determined by the guidance of the arrangement of the cells in Stratum cellulare externum. The lateral part of the medial column (M. c., l. Fig. 85) is still composed of comparatively few cells, which form a lesser cellular condensation.

The lateral column is on the contrary, a compact and more peripheral projecting cellular mass (compare *Acanthias*, stage 3,9 cm. [Fig. 57]).

*Stage 1,3 cm.* (Fig. 86). A considerable differentiation has taken place at this stage. In the ventral part (V. c. Fig. 86) the Nucleus III (Nc. III Fig. 86) has become fully visible, and ventral and somewhat lateral to this nucleus, Nucleus ruber (Nc. r. Fig. 86). Near the medial-line the cells lie more compactly than at the preceding stages, and form a dorso-ventrally extended nucleus connected with the ventro-lateral part of the ventral column (V. c., vl. Fig. 86). This latter part is vigorously developed.

In the medial part the cells nearest to the Stratum cellulare internum ("Centrales Höhlengrau") lie comparatively far from each other and are, as at previous stages, disposed reticularly. Outside these cells is found a cell-condensation in almost the same position as the cell-group *m* Fig. 83 in *Gallus*. There is likewise at stage 1,3 cm. an already powerfully developed cell-agglomeration in the periphery of the medial part. This is the oriment of the Substantia nigra (S. n. Fig. 86). A comparison with *Gallus* embryos at stages 9—10 days shews, that the correspondence, at least in appearance and position, between the mesencephalic part of the Ganglion opticum basale (EDINGER) and Substantia nigra is very considerable.

In the lateral part I have been unable to observe any cell-condensation whatever. On the other hand such a condensation is to be found in the dorsal part (D. c. Fig. 86).

As no important changes have taken place at stage 1,6 cm., I pass over to a description of *stage 1,9 cm.* (Fig. 87). Substantia nigra (S. n. Fig. 87) has grown and become covered with a distinct fibre-layer: the Pes pedunculi. The cell-condensation lateral to the Nucleus ruber (Nc. r. Fig. 87) is decidedly less distinct.

Peripherally in the lateral part (L. c. Fig. 87) the number of cells is certainly greater than at previous stages. The cells however do not lie so compactly as in the Substantia nigra and in the peripheral cell-condensation in the dorsal part (D. c. Fig. 87).

Through the outward curving of the dorsal part (Brachium corp. quadr.

post.) a groove (Fissura interbrachialis) has appeared between it and the Tectum-formation. This same groove exists, as a matter of fact, already at stage 1,6 cm. and there are traces of it even earlier. In the centre of the dorsal part can be discerned a cell-mass, namely a column, which together with the peripheral cellular mass, caudally merges into the nucleus of the posterior Colliculi.

I have not been able to discover a nucleus in *Mus*, any more than in *Rana* or *Gallus*, which could be considered homologous with the "Geniculatum laterale" in *Acanthias*. The mammalian Corpus geniculatum mediale, which WALLENBERG (1907) has with some hesitation termed homologous with this *Acanthias* nucleus, clearly lies in and is formed from the Diencephalon in *Mus*.

#### 4. THE CORPUS QUADRIGEMINUM POSTERIUS.

According to KAPPERS (1906, 1907), the Tori semicirculares corresponds with the posterior Colliculi in mammals. He (1907) writes: "Bei den Amphibien entwickeln sich die Tori semicirculares in auffallender Weise, denn, während sie in ihrem frontalen Teile dort dem Typus der Teleostomi beibehalten, verwachsen sie, weil keine Valvula sie trennt, in ihrem mittleren Teile mit der medialen Wand untereinander und teilen so den Ventriculus opticus in zwei kleinere Ventrikel, wovon der obere die Fortsetzung des optischen Ventrikels ist und überdacht wird vom Tectum, während der untere, der gleich mit der Sylvischen Wasserleitung kommuniziert, hier schon als *Ventriculus corporis quadrigemini posterioris* zu bezeichnen ist" (page 470).

As Torus semicircularis is to be found in all the vertebrates except mammals, it is now generally considered homologous with the Corpus quadrigeminum posterius in works of reference on the subject. By a comparative embryological investigation of the caudal part of the Mesencephalon in *Acanthias*, *Salmo*, *Rana*, *Gallus* and *Mus*, I have come to a conclusion differing from the above.

In *Mus* at stage 0,8 cm. there has developed, caudally in the roof of the mid-brain two sacs or recesses (R. p. m. Figs. 34, 88), the Recessi

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Fig. 87. Transverse-section through the mid-brain of *Mus* at stage 1,9 cm. Fig. 88. Horizontal section through the mid-brain of *Mus* at stage 0,8 cm. Fig. 89. Horizontal section through the mid-brain of *Acanthias* at stage 15,0 cm. Fig. 90. Horizontal section through the mid-brain of *Rana* at stage 0,7 cm. Fig. 91. Horizontal section through the mid-brain of *Salmo* at stage 0,8 cm. (Microphotographs.)

C, Cerebellum; C. p., Commissura posterior; D. c., the dorsal part; L. c., the lateral part; M. c., the medial part; Nc. III, Nucleus oculomotorius; Nc. r., Nucleus ruber; R. p. m., Recessus posterior mesencephali; S. l. v., Sulcus longitudinalis ventralis; S. n., Substantia nigra; T. o., Tectum opticum; V. c., the ventral part; vl., the ventro-lateral portion of the ventral column.

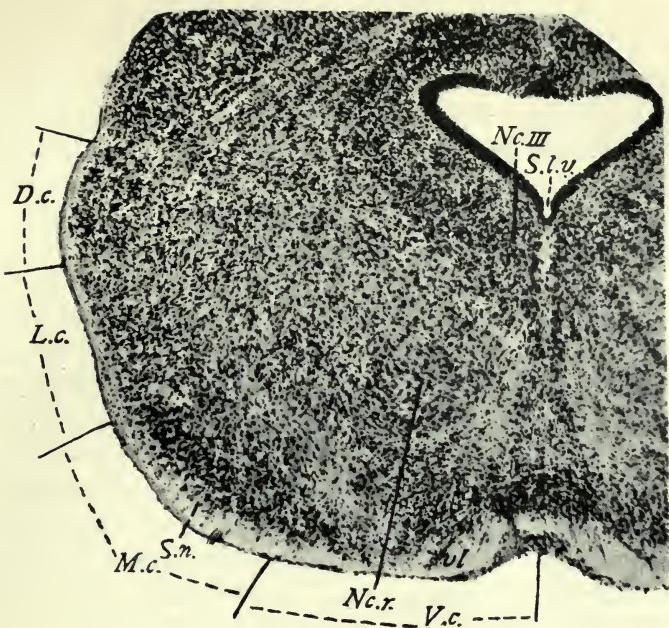


Fig. 87.

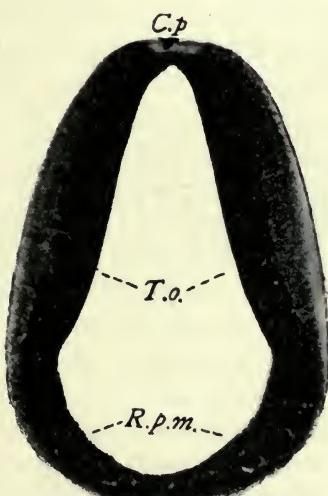


Fig. 88.

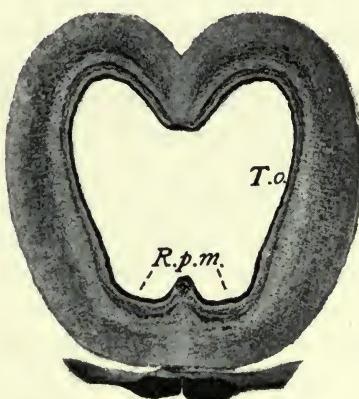


Fig. 89.

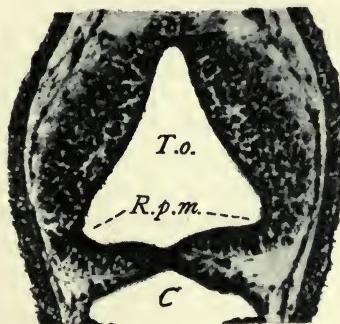


Fig. 90.

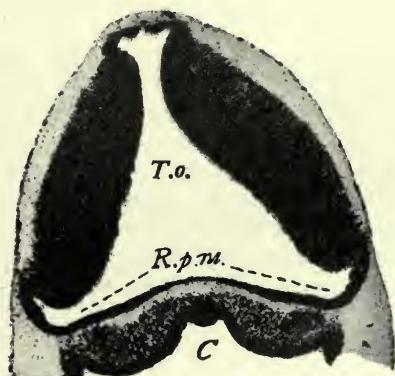


Fig. 91.

posterores mesencephali of the authors. Along the lateral walls of each of these recesses, has formed a horizontal groove, which is connected neither with the Sulcus lateralis tecti nor with the Sulcus intraencephalicus. With the guidance of this groove it becomes possible to subdivide the caudal part of the Mesencephalon into a ventro-caudal and a dorsal portion. Not until the development of the outer groove, which separates the anterior from the posterior Colliculi, has taken place, can the boundary of the dorsal portion (Colliculus inferior) be sharply defined from the Tectum opticum, viz. Colliculus superior. The ventro-caudal portion extends down to the Fissura rhombo-mesencephalica. The dorsal part of the Sulcus intraencephalicus posterior can also serve as boundary-mark between this portion and the Metencephalon.

Already at stage 0,8 cm. and later still more clearly defined, there is a histological difference between the dorsal roof-portion and the ventro-caudal portion that only consists of a compact neuroblastic layer (comp. Fig. 94). The wall is, moreover, comparatively thin.

On comparing the Tectum with this roof-portion, it will be found that a histological difference is likewise to be noticed here. A peripherally compact cell-layer has developed in the Tectum, but does not extend into the Colliculus inferior (Fig. 94). Further the Tectum (T. o. Fig. 94) is thicker than the roof of Colliculus inferior (C. q. p. Fig. 94).

In the fully developed brain (and even in young animals of 4,0 cm. in length) almost the whole of the ventro-caudal portion is reduced to a thin membrane (Fig. 95), which is non-nervous until the point where it passes into the roof-portion. Thus it is chiefly the dorsal, or that part of the caudal part of the Mesencephalon, lying dorsal to the Ventriculus corporis quadrigemini posterioris (V. c. q. p. Fig. 95), which develops into the so-called Colliculus inferior (C. q. p. Fig. 95). That portion that lies ventro-caudal to the ventricle or ventricle-groove, becomes reduced<sup>1</sup>, and forms, the anterior part of the Velum medullare anterius<sup>2</sup>.

After this summary description of the development of the posterior colliculi in *Mus*, I will pass on to the lower vertebrates, commencing with:

*Amphibia*. Already early in the embryonic development of the frog (stage 0,7 cm. [Fig. 90]) the Tectum in horizontal sections has the form

<sup>1</sup> At stage 2,3 cm. the absolute length of the ventro-caudal portion is about 2½ times larger than the length of the nervous part of the same portion at stage 4,0 cm.

<sup>2</sup> The term Velum medullare anterius should, by rights, refer to that part of the connecting part between the mid-brain and Cerebellum, which lies between the Fissura rhombo-mesencephalica and the anterior border of the Cerebellum. I cannot determine where the boundary-line between Mes- and Metencephalon in Velum in the fully developed brain, should be drawn, since Fissura rhombo-mesencephalica no longer exists. It is however probable, that it lies as at the embryonic stages, immediately frontad of the decussation of the trochlear nerve.

of a triangle with the angle pointing frontad. A comparatively thin wall forms the base of this triangle, at the angles of which the roof of the Mesencephalon forms a pair of recesses (R. p. m. Fig. 90). The caudal wall of these recesses, which is comparatively thin, and has, moreover, no peripheral fibre stratum, extends down to the Fissura rhombo-mesencephalica. The roof portion of the recesses is somewhat thicker, but thinner than the Tectum further frontad.

In consequence of the correspondence, as well in the structure of the walls, as in the general form, these posterior recesses can be considered homologous with the two Recessi posteriores mesencephali (Ventriculi corp. quadr. post.) in mammals.

Towards the end of the larva-stage, the Tori semicirculares begin<sup>1</sup> in consequence of their increase in size, to grow together caudally at the medial-line.

This does not cause, however, a division of the Ventriculus opticus into two parts, as the Torus (T. s. Fig. 96) lies close to the boundary-plane between the Mes- and Metencephalon, directly dorsal of the Sulcus intraencephalicus (S. i. p. Fig. 96) and Fissura rhombo-mesencephalica. The Torus semicircularis, on other words, lies in the caudal wall of the recesses, while an equivalent to the Colliculus inferior is to be sought in the roof portion (comp. Figs. 94, 95, 96).

HERRICK (1917) has newly published a work on the mid-brain and thalamus of *Necturus*, in which he divides the Tectum into two parts: Colliculus superior and Colliculus inferior. The former part "is reached by the optic tracts and this part may therefore be termed tectum opticum and considered homologous with the mammalian colliculus superior" (page 283). This part "does not extend backward to the caudal end of the tectum" (page 245). Behind the same lies the Colliculi inferiores. HERRICK is unable to draw a boundary-line between these parts. With regard to the caudal wall of the recesses, HERRICK says: "In adult *Necturus* the recess is contracted except under the extreme caudal end of the tectum, where the roof is thin and non-nervous forming a small velum medullare anterius" (page 224). This Velum medullare anterius should thus answer to the mesencephalic part of the Velum, i. e. the part that lies in front of the decussation of the Nervus trochlearis.

*Salmo* (Fig. 91) corresponds with *Rana*, although the Tori semicirculares have not, as is known, grown together caudad in the medial line. In

<sup>1</sup> Since the lateral column in Amphibia and Birds, which also belongs to the Torus semicircularis, ceases later at the boundary-plane between the Mes- and Metencephalon, it is clearly only the Torus-formation proper, that is to say, the dorsal part of the Subtectum that continues into the caudal part of the mid-brain which projects over the Velum.

*Salmo*, the caudal wall of the recesses soon becomes very thin and epithelial. Whether a part answering to the posterior Colliculi exists in the roof-portion of these recesses could only be proved in the same way as HERRICK (1917) did in the case of *Necturus*, i. e. by analysis of the fibre anatomy. On haemalum-preparations I have not been able to discover any caudal part diverging histologically from the Tectum opticum.

In *Gallus* at the 8 day stage (Fig. 92) are to be found a pair of well-developed Recessi posteriores mesencephali (R. p. m.). The wall of these recesses is decidedly thinner than in the rest of the Tectum. This is especially the case in the ventro-caudal wall. Already at the 8½ day stage these recesses (R. p. m. Fig. 93) become considerably smaller, at the 9 day stage can hardly any longer be traced, and disappear subsequently altogether. At the 8 day stage they lie in the caudal part of the roof of the mid-brain. In consequence of the considerable modifications in form, which take place at the following stages, they become displaced nearer the medial line, which appears from a comparison between Figs. 92 and 93. If Colliculi inferiores exist in Birds, they should consequently be sought caudally and medially in the roof of the mid-brain.

The position of the Torus semicircularis in relation to the Recessus posterior mesencephali and the boundary-plane between the mid- and hind-brain is the same as in *Rana* (comp. Figs. 96, 97). In Reptiles it seems to be so too.

In *Acanthias*, on account of the lack of material at suitable stages (5—8 cm.), I have not been able to study closely the development of the part of the mid-brain in question. A faint indication of caudal recesses seems however to exist at stage 15,0 cm. (Fig. 89). On the other hand, the caudal part of the Tectum is at least at this stage not thinner.

The Torus-formation in *Acanthias* is, as above mentioned (p. 44), divided into: an anterior part in which the histological structure is that characteristic for the Torus-formation, and a posterior part, more closely-cellulated,

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Fig. 92. Horizontal section through the mid-brain of *Gallus* at stage 8 days. Fig. 93. Horizontal section through the mid-brain of *Gallus* at stage 8½ days. Fig. 94. Parasagittal section through the posterior part of the mid-brain of *Mus* at stage 2,3 cm. Fig. 95. Parasagittal section through the posterior part of the mid-brain of *Mus* at stage 4,0 cm. Fig. 96. Parasagittal section of *Rana* at stage 3,6 cm. Fig. 97. Parasagittal section through the posterior part of the mid-brain of *Gallus* at stage 8 days. (Micro-photographs.)

C, Cerebellum; C. p., Commissura posterior; C. q. p., Corpus quadrigeminum posterius; F. rh. m., Fissura rhombo-mesencephalica; I, the infundibular region; M, Mesencephalon; P. dm., Prominentia dia-mesencephalica; R. p. m., Recessus posterior mesencephali; S. i. p., Sulcus intraencephalicus posterior; T. o., Tectum opticum; T. s., Torus semicircularis; V. c. q. p., Ventriculus corporis quadrigemini posterioris; V. m. a., Velum medullare anterius.

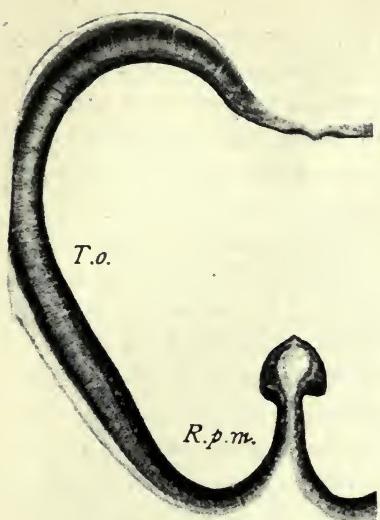


Fig. 92.

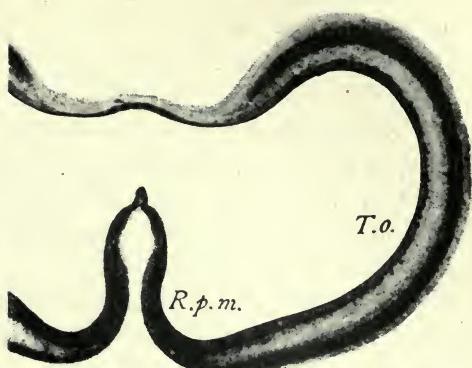


Fig. 93.

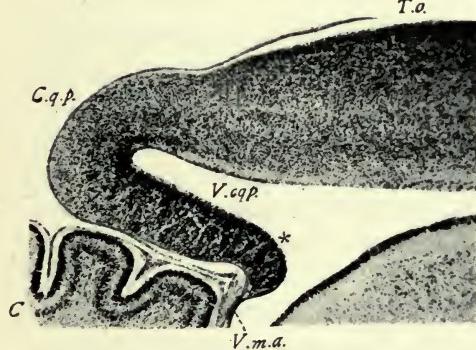


Fig. 94.

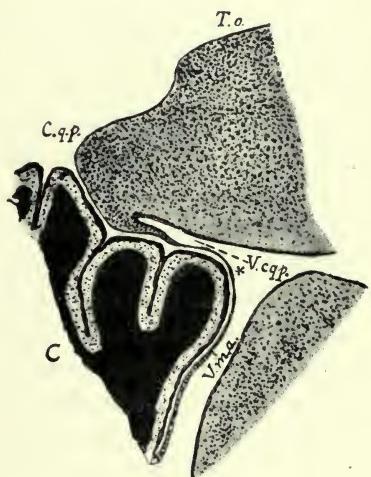


Fig. 95.

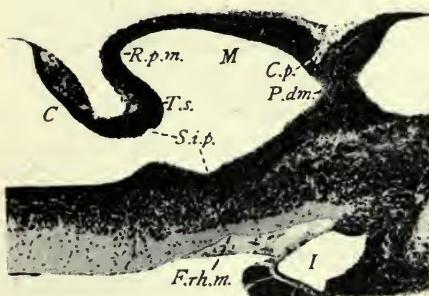


Fig. 96.



Fig. 97.

which extends towards the Velum medullare. The boundary between these parts coincides with the boundary between the recesses and the anterior part of the Tectum. On parasagittal sections the caudal part of the Torus-formation (p. T. f. Fig. 98) can be proved to lie in the most caudal part of the mid-brain, i. e. close to, and dorsal to the Fissura rhombo-mesencephalica (F. rh. m. Fig. 98) and Sulcus intraencephalicus. The part of the Tectum, where this Torus-formation is found and where the disposition of cells in Stratum cellulare externum is not that typical for the rest of the Tectum, can therefore be said to be homologous with the ventro-caudal wall of the Recessi posteriores mesencephali. Dorsal to it however, no differentiated indication of posterior Colliculi can be discovered, at least, not in cresyl-violet preparations.

A correspondence to this specially differentiated posterior part of the Torus-formation appears to exist in *Gallus*. The typical Torus-formation is here caudally in contact with a compact cellular mass (p. T. f. Fig. 99), belonging to the Stratum cellulare internum. This cellular mass occupies the same morphological position as the caudal part of the Torus-formation in *Acanthias*.

There is, as is well known, no developed Torus-formation in mammals, but if there were, it would assuredly lie at \* Figs. 94, 95 (comp. Figs. 94—97).

The Nucleus colliculi inferioris is an enlarged caudal part of the cell-mass in what I have called the dorsal part, i. e. Brachium quadrigeminum inferius. No such larger caudal part of the Stratum cellulare externum of the dorsal part, namely the dorsal column, is to be found in the lower animal types examined by me. In all these the dorsal column is less prominent caudally than further frontad.

In Selachii (*Acanthias*) the caudal part of the Torus-formation presents, to be sure, a superficial likeness to the Nucleus colliculi inferioris, but is certainly not to be compared with the latter. WALLENBERG (1907) describes and figures a nucleus ("Mittelhirnhaubenkern") in *Torpedo*, which has: "eine grosse Ähnlichkeit mit dem Corpus bigeminum posterius niederer Säuger" (page 389). The figure 32a is unfortunately so schematic, that it is not possible for me to decide which portion of the dorsal part this nucleus would correspond with in *Acanthias*.

## 5. CONCLUSIONS.

In earlier ontogenetic stages the Subtectum, i. e. the basal portion of the Mesencephalon, is, on the whole, similarly constructed in all the animal types examined by me. A comparison made between *Acanthias*, *Gallus* and *Mus*, most plainly proves this agreement.

In that part I call the ventral we find the Nuclei oculomotorii, which

in all the types investigated form the Stratum cellulare internum. In Stratum cellulare externum a medial cell-group, a superficial ventro-lateral, as also a lateral ditto can be discerned in *Acanthias* at stage 5,0 cm. (Fig. 58), in *Gallus* in the 6 day stage (Fig. 78), and in *Mus* at stage 0,8 cm. (Fig. 84). In the ventro-lateral and lateral portions the cells are horizontally arranged. In *Saimo* and *Rana* this part is so devoid of cells that it is scarcely possible to discern any definite groups of cells. In *Acanthias* and *Gallus* the medial group of cells becomes extremely diffuse in later stages. In *Mus* the number of cells in this portion is relatively large. The ventro-lateral group disappears as such in the later stages in *Acanthias* and *Gallus*. In *Mus* it is retained very evidently, at any rate up to the 1,9 cm. stage. Finally the lateral group (in *Gallus* and *Mus*) is included in the formation of Nucleus ruber.

A Nucleus ruber has been described in fishes (Selachians [WALLENBERG, 1907], Ganoids [JOHNSTON, 1901], Teleosts [GOLDSTEIN, 1905]). De LANGE (1913) has written about a number of large reticular cells in the ventral portion of the mid-brain in Selachians (and all groups of fishes) and Amphibians (*Rana*), as "prototype des Nucleus ruber". He has also (1912) found a red Nucleus in Reptiles. In the ontogenetic stages of fishes and *Rana* investigated by me these large cells could not be identified, and their embryological origin was therefore not studied.

In *Gallus* and *Mus*, where I could follow the development of the Nucleus ruber, there is at certain intermediate stages (in *Gallus* in the 7 day stage [Fig. 79], in *Mus* at stage 1,0 cm. [Fig. 85]) a cell-mass that appears to be formed partly from Stratum cellulare internum immediately dorsal to the Fasciculus longitudinalis dorsalis, partly from the lateral group of cells in the ventral part. (A similar group of cells is found also in *Acanthias* in the 5,0 cm. stage [Fig. 58].) In *Gallus* this cell-group projects somewhat into the medial part, i. e. the boundary between the ventral column and the medial is no longer discernible, or is indistinct. The boundary-line between the ventral column and the medial is, however, immediately median of a condensation in the lateral portion of the cell-group in question, though it cannot be discerned in the Stratum cellulare externum. The same boundary-line, even if not so very distinctly, is also noticeable in later stages (8—9 days). The Nucleus ruber is formed (in the stages 9—15 days) from the cell-mass median to the boundary-line. The Nucleus ruber in *Gallus* is formed in the ventral part. In *Mus* it seems to be so too.

As belonging to the medial portion I have assigned the very characteristic and rather constantly occurring thickening in the Stratum cellulare internum. In *Acanthias*, *Gallus* and *Mus*, the medial column is more or less plainly divided into two portions.

In *Acanthias* the division is distinct only in the stage 3,9 cm. (Fig. 57). In *Gallus*, on the contrary, up to the 15 day stage. In both these forms the

medial portion is more abounding in cells than the lateral. In *Gallus* a nucleus (the Ganglion profundum mediale [EDINGER, 1908]) is formed in the medial portion that appears to have a partial equivalent in *Mus*. In *Mus*, at stage 0,8 cm., the medial portion of the medial column abounds more in cells than the lateral, this being also the case in *Acanthias* and *Gallus*. Already in stage 1,0 cm., however, the number of cells in the lateral portion has increased, so that this portion is almost as profuse in cells as the medial. By the coalescence of these two portions a nucleus (the Ganglion profundum laterale, EDINGER [1911]) is formed, the position of which, as regards Nucleus ruber and Substantia nigra, is almost the same as that nucleus designates *m* in Fig. 83 (Ganglion profundum mediale) in *Gallus* in relation to the Nucleus ruber (Nc. r.) and Nucleus ectomammillaris (Nc. e.)<sup>1</sup>.

In *Salmo* and *Rana* the medial column is undivided.

In the periphery of the medial part of all those animal types investigated there occurs a group of cells that in *Mus* forms the Substantia nigra. In *Acanthias* (Fig. 58) the number of cells in the periphery of this part is relatively small. In *Salmo* (Figs. 72, 73), but only in the embryos, there is a large peripheric nucleus, or cell mantle, in the medial portion of which cells enter that formed from the medial part. In *Rana*, as early as in stage 3,6 cm. (Fig. 75), and later on still more plainly, you discern how the medial column becomes more dense towards the periphery and forms the posterior part of a nucleus that GAUPP (1899) designated Nucleus ectomammillaris. The nucleus that in *Gallus* (Figs. 81—83) appears in the periphery of the part in question has been described by EDINGER as Nucleus ectomammillaris (Ganglion opticum basale, Nucleus peduncularis of BELLONCI [1888]). It is however evident that the real Nucleus ectomammillaris belongs to the Diencephalon. Thus for instance in Teleosts (EDINGER [1908]), as also in Reptiles and birds. The Nucleus ectomammillaris, figured by EDINGER in his work "Studien über das Zwischenhirn der Reptilien" (1899), is evidently in the Diencephalon. Judging from EDINGER's Fig. 159 in his "Vorlesungen, etc." (1908) he has also assigned the mesencephalic nucleus in question as belonging to the Nucleus ectomammillaris. TURNER (1891) designates the Nucleus ectomammillaris "Nidulus inferius" and says: "This

<sup>1</sup> According to Edinger (1908, 1911) the Ganglion mesencephali profundum mediale and laterale are present in all Vertebrates. In fishes, Amphibians, birds (and Reptiles?) the lateral column seems to be what Edinger names Ganglion mesencephali profundum laterale. In fishes and Amphibians the medial column probably is synonymous with the Ganglion mesencephali profundum mediale. In birds (and Reptiles?), however, it is the medial part of the medial column that Edinger names the Ganglion mesencephali profundum mediale. In man, at last, the Ganglion mesencephali profundum laterale lies immediately lateral and the Ganglion mesencephali profundum mediale medial to the Nucleus ruber. Thus Edinger has named very different nuclei with the same terms.

Nidulus extends from the junction of the Mesencephalon with the Metencephalon cephalo-mesad about half-way to the optic chiasma" (p. 121).

In older embryos, certainly, the diencephalic and mesencephalic portions of the Nucleus ectomammillaris are coherent with each other, but in the earlier stages a boundary between them may easily be discerned.

As in *Rana* (Fig. 75), during the larval stages, the number of cells in the nucleus is relatively small, I have been unable to discover any certain line of demarcation between the posterior mesencephalic and the anterior diencephalic portion.

The posterior mesencephalic portion of the Nucleus ectomammillaris in *Rana* and *Gallus* is formed in the medial part, and are, moreover, in the same position as the oriment of the Substantia nigra in mammals. These nuclei are probably homologous. The Substantia nigra merge, however, later with a cellgroup that belongs to the ventral part (Fig. 87). The Substantia nigra has by BAUER (1909) previously been deemed homologous with the Nucleus entopeduncularis (EDINGER). This is, however, entirely a diencephalic nucleus<sup>1</sup>.

Likewise, in the lateral part, an inner cell-mass and an outer peripheric nucleus may be distinguished. In the earlier stages the lateral column in all the forms (with the exception of *Salmo* and *Rana*) consists of a dense mass of cells, rather large, and often projecting somewhat farther towards the periphery than the medial column. In the later stages in *Acanthias* a peripheric and very distinct nucleus forms in this part (Fig. 59). From the lateral part, even in *Salmo* (Figs. 72, 73), cells proceed that enter into the construction of the above mentioned peripheric cell-mantle. In *Gallus* as in *Mus* the number of cells in the periphery are considerably less in the lateral than in the medial part. It is however possible to discern a slight cell-condensation in the periphery of the lateral part in *Gallus* in the 15-day stage (Fig. 83) and in *Mus* in the 1,9 cm. stage (Fig. 87).

The mesencephalic part of the Substantia reticularis lies in the inner portion of the lateral as well as of the medial part, close to the Stratum cellulare internum.

The dorsal part is at first indistinctly separated from the adjoining parts (Tectum opticum, and the lateral part). Soon, however, a differentiation occurs. In the Stratum cellulare internum what I designate as the Torus-formation appears, and to this I assign 1) the Nucleus lateralis mesencephali, in accordance with the more limited definition of this nucleus I have introduced and 2) a denser, semicircular cell-mantle, of the Stratum cellulare internum, that in certain forms (e. g. *Acanthias* and *Gallus*) is plainly visible in certain stages. In *Acanthias* (Fig. 59), this Torus-formation completely

<sup>1</sup> Comp. also HERRICK (1891, 1892, a, c).

fills the Torus semicircularis.<sup>1</sup> Already in the Ganoids and Teleosts the lateral column is partly in the Torus semicircularis. In Amphibians and still more plainly in birds, the lateral part lies entirely within the Torus semicircularis, which is therefore not fully homologous in the various groups of vertebrates.

The cell-mass that in *Acanthias* (in the stages 5,0 to 15,0 cm. [Figs. 58, 59]) fills the intermediate space between the Torus-formation and the optic tract I name the dorsal column. In *Salmo* (Fig. 71), from the neuroblastic stratum in the dorsal part, a cell-group is formed which I consider corresponds to the dorsal column in *Acanthias*. This cell-group may be traced frontad to the region where the Torus lateralis is formed later on (Figs. 67, 68). In the dorsal part of the Torus lateralis cells enter formed from all the parts of the Subtectum, with the sole exception of the ventral. This dorsal portion of the Torus lateralis, owing to the corresponding position and manner of formation, I have homologized with the "Corpus geniculatum laterale" in Selachians. The nucleus last-mentioned is not homologous with the Geniculatum laterale in Teleosts. I have found no correspondence to the Selachian "Geniculatum" in the higher animals (amphibians, birds, mammals).

In later stages we may distinguish in *Salmo* (Figs. 72, 73) a peripheric part, disappearing subsequently, in the dorsal column. This column in *Rana* consists simply of a very small number of cells. In *Gallus* the dorsal column in younger stages (6 to 10 days [Figs. 80—82]) is but little conspicuous. Owing to the cells therein increasing in size by growth later on, a visible nucleus (Fig. 83 D. c.) is formed, however, which TURNER (1891) has described and figured under the denomination Nidulus lenticularis.

The nucleus (\* Fig. 83) that in *Gallus* in the 15-day stage lies in the optic tract has scarcely any equivalent in the mid-brain of the other groups of animals. In *Mus* the dorsal column divides into a superficial condensation and a central nucleus that together form the grey matter of the Brachium colliculi inferioris. The posterior portion of the dorsal column in mammals has developed to the so-called Corpora quadrigemina posteriores (Nucleus colliculi inferioris).

In a suitably orientated series of cross sections of *Acanthias* in the stage 3,9 cm. it may be ascertained that the thickened Stratum cellulare internum of the medial part, as also the entire medial column continues in the Metencephalon and Medulla oblongata, lying there inside the Funiculus medialis. The medial column extends therefore into the ventral column in the Medulla and the spinal cord. To this we must also assign the ventral part in the mid-brain. In the Medulla this part is very inconsiderable and only in certain portions (e. g. at the Ganglion interpedunculare) does it

<sup>1</sup> In Selachians (*Galeus*) a Torus semicircularis has previously been described by KAPPERS (1906).

contain larger accumulations of cells. The medial and ventral parts may therefore be said to correspond to the ventral column of the Medulla and spinal cord. So far as I can ascertain the lateral column in the Mesencephalon forms a continuation of the lateral column in the spinal cord. That the dorsal column apparently comes to an end in Mesencephalon, i. e. that it projects upwards dorsal to the Fissura rhombo-mesencephalica, need evidently not necessarily signify that it is devoid of an equivalent in the Medulla and the spinal cord. It simply shows that a corresponding column is lacking in the isthmus region, i. e. beneath the Flica encephali dorsalis.

The Mesencephalon may thus be stated to consist of four chief portions, viz. 1) Tectum opticum; 2) The dorsal part of the Subtectum with Corpus quadrigeminum posterius; 3) The lateral part, and 4) The medial part inclusive of the ventral. Naturally it is a difficult thing to definitely decide whether these four portions correspond to the four functional portions into which the spinal cord and the oblongata have been divided. Should this be the case, however, it would provide a good starting-point for the functional division of the Mesencephalon.

## II. THE CEREBELLUM.

Cerebellum has been studied in *Acanthias vulgaris*, *Acipenser ruthenus*, *Lepidosteus osseus*, *Salmo salvelinus* and *Osmerus eperlanus*.

*A. Selachii*: The structure of the Cerebellum is well-known, thanks to the investigations of BURCKHARDT (1897), EDINGER (1901), VOORHOEVE (1917) and others.

Cerebellum is usually divided into a medial: Corpus cerebelli and two lateral parts: Auriculi cerebelli. As these latter are connected by a medial caudal part, which I will call: Pars medialis auriculi, it would be suitable to make a distinction between an anterior part: Corpus cerebelli and a posterior: Pars auricularis. The auricles consist of two laminae, an outer and an inner. I term them: Lobus externus and internus auriculi.

According to VOORHOEVE (1917) the Auriculi are separated from the Corpus by two lateral grooves, the Sulci paraauriculares, which are connected with a medial groove: Sulcus postremus. In front of this groove lies another medial one: Sulcus posticus. This groove can, especially in older specimens of *Acanthias*, be traced frontad and laterad, and there form the dorsal boundary of a laterally projecting part of the Corpus. Moreover, since Sulcus paraauricularis and Sulcus postremus are already developed at stage 6,5 cm., but Sulcus posticus first appears at stage 15,0 cm., the first mentioned grooves may be considered as the true boundary grooves between the Corpus and Pars auricularis.

The granular cells in Selachians are, as is known, principally concen-

trated in two longitudinal strings or ridges ("Kleinhirnlippe") (S. g. c. Fig. 106), one on each side of a paired ependymal thickening (E. th. Fig. 106). These strings of granular cells can be traced from the Decussatio veli viz. the decussation of the Nervus IV, through Corpus and the part between Sulcus posticus and Sulcus postremus and then along the caudal surface of the Pars medialis auriculi. After this the strings separate and form together with a Purkinje-cell- and a molecular-layer the edges of the Lobi interni and externi.

These strings extend therefore without interruption through the whole of the Cerebellum and behind it along the edges of the Fossa rhomboidalis. It is however worthy of mention, that in older embryos of *Acanthias* (15,0 cm.) and in full-grown animals, there exist two very well-defined transverse grooves, which cut fairly deeply into the strings at a point which lies opposite the Sulcus postremus. These grooves certainly appear comparatively late, but are, as far as I could find, invariable in occurrence and position. It seems therefore probable that these grooves are to be considered as boundary-grooves between the Corpus and Pars auricularis viz. Pars medialis auriculi.

Scattered granular cells are also to be found here and there in the cerebellar substance (EDINGER [1901]).

B. Ganoidei. a) *Acipenser ruthenus*. The Cerebellum has been investigated in *Acipenser* by GORONOWITSCH (1888) (*A. ruthenus*) and JOHNSTON (1898, 1901) (*A. sturio*).

Cerebellum in *Acipenser* can likewise be subdivided into a medial part: Corpus, and two lateral parts, Auriculi cerebelli (Pedunculi cerebelli of GORONOWITSCH). Between the Corpus and Lobi interni auriculi (Fimbria of GORONOWITSCH, the lateral lobes of JOHNSTON) have developed longitudinal grooves (S. p. Figs. 103, 104), which are clearly identical with the Sulci paraauriculares (Voorhoeve) in Selachians. No Sulcus postremus i. e. no boundary-groove between Corpus and Pars medialis auriculi has on the contrary been described.

GORONOWITSCH (1888), however, describes "in den distalen Abschnitten des dorsalen Teiles des Körpers ein stark entwickeltes Querfasersystem, welches das Körnergewebe der Fimbria beider Seiten mit einander verbindet" (page 536). JOHNSTON (1901) says: "The cerebellar crest — — — is not lost as a distinct bundle, but continues mesially and then caudo-mesially along the border of the lateral lobes at their junction with the plexus chorioideus, and finally forms the most caudal and dorsal portion of the molecular layer in the middle line" (page 90). This caudal and dorsal portion of the Cerebellum can be indicated as Pars medialis auriculi. I am not able to draw up a boundary between this portion and the Corpus, as I have only had a series of transverse sections at my disposal.

According to GORONOWITSCH and JOHNSTON, a large granular cell-mass

## STUDIES ON THE MID-BRAIN AND CEREBELLUM

(Seitenwulst of GORONOWITSCH) lies on each side of the great medial molecular mass in the Corpus. These lateral granular cell-agglomerations extend into the Valvula cerebelli and also cover the frontal parts of the Auriculi cerebelli. Granular cell-strings are further found along the Lobi interni and externi as well as along the Crista cerebelli. These granular cell-strings are connected with the granular cell-agglomerations in the Corpus at the frontal parts of the Auriculi.

*Fig. 100, section 227<sup>1</sup>.* Represents a section through the most caudal part of the Cerebellum viz. Pars medialis auriculi. Granular cells (s. g. c.) here cover the ventral and lateral walls of this part in a continuous layer.

*Fig. 101, section 212.* The granular cells form two strings on each side: a lateral (l. s. g. c.) and a medial string (m. s. g. c.). These strings become fused caudally, i. e. merged into each other (Fig. 100 s. g. c.).

*Fig. 102, section 186.* The lateral as well as the medial strings remain (l. s. g. c. and m. s. g. c.). The latter lie in a "prominent median ridge" (JOHNSTON), the "Kiel" of GORONOWITSCH (K), but have not been described or figured by these investigators. The bulk of granular cells forms the two great cell-agglomerations (g. m.) one on each side of the Corpus between the above mentioned strings. The Crista cerebelli is further covered by a granular cell-string.

*Fig. 103, section 115.* The lateral cell-agglomerations have been subdivided into a dorsal (l. g. m.) and a ventral part (c. g. m.), which are clearly separated from each other. The dorsal agglomeration lies in the Lobus internus (L. i.), the ventral in the Corpus. The section has, to the right on Fig. 103, touched the point of fusion between Lobus internus and externus. The lateral granular cell-string (l. s. g. c.) here passes continuously into the granular cell-string in Crista cerebelli, respectively Lobus externus. The medial strings (m. s. g. c.) are to be found again in the median ridge, but are now somewhat smaller than further caudad.

*Fig. 104, section 101.* This section is on the right of the figure tangent to the Recessus lateralis (R. l.). On the opposite side the section has intersected the auricle further caudad. Here the anterior part of the granular cell-strings of the auricles is still visible (l. s. g. c.). In the left auricle (to the right of the figure) there appear only two larger granular cell-agglomerations. The dorso-lateral is the same as that represented on Fig. 103 l. g. m. The ventro-lateral continues caudad and lies under the Crista cerebelli (Fig. 103)<sup>2</sup>. Both these agglomerations, which are seen to merge continuously

<sup>1</sup> In the series of sections I have examined, the thickness of the sections was 25  $\mu$ . The number of sections into which Cerebellum was cut was 235. Fig. 100 represents the 227<sup>th</sup> section.

<sup>2</sup> This ventral granular cellular tissue is clearly that described by GORONOWITSCH as: "die ventrale Körnerlage" (p. 536) and by JOHNSTON (1898) as *Tuberculum acusticum* (p. 586).

into each other in Fig. 105 l. g. m., cannot according to me, be said to be in continuous connection with the granular cell-strings of the auricles. These latter consist of very closely-packed cells. There are indeed, scattered granular cells between these strings and the just mentioned cell-agglomerations, but no true fusion takes place. While the granular cell-strings thus form the edges of the Lobi and cover the inner wall of the Recessi laterales, the remaining granular cell-agglomerations lie on the frontal surface of the auricles, in the medial part of Lobi interni and ventral to Crista cerebelli.

*Fig. 105, section 82.* This section is tangent to the frontal part of the Auriculi, where the above mentioned granular cell-agglomerations merge continuously into each other. The granular cell-agglomerations in the Corpus (c. g. m.) continue frontad and into the Valvula cerebelli, where they lie in the same position as in the Corpus. The medial strings (m. s. g. c.), on the contrary, do not extend into the Valvula, but finish with a number of small groups of cells, irregularly scattered about in the ventro-lateral parts of the median ridge.

On section 115 (Fig. 103), the molecular layer (M. l.) is visible, partly in the Lobus externus, ventral to the granular cell-string, partly on the dorsal side of the Lobus internus. In both these parts the dendrites of the Purkinje-cells seem to lie in more regular order than in the medial molecular-mass and in the median ridge. Between the molecular layer in the Lobus internus and the more medial parts, it is therefore possible to draw a sharp boundary-line. By following the series of sections frontad, it is possible to see how the fusion of the molecular layers takes place (Figs. 104, 105), and forms a mantle dorsal to the large cell-agglomeration (l. g. m.). If section 82, Fig. 105 is now compared with a section which is tangent to the auricles in *Acanthias* (Fig. 106), it becomes clear that the fused granular cell-strings (s. g. c. Fig. 106) in this species cannot be directly compared with the granular cell-agglomerations in *Acipenser* (l. g. m. Fig. 105). The molecular layer (M. l.) lies ventral to the granular cells in *Acanthias*, but

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Fig. 98. Parasagittal section through the posterior part of the mid-brain of *Acanthias* at stage 15,0 cm. (Microphotograph.) Fig. 99. Transverse-section of posterior part of the mid-brain of *Gallus* at stage 8 days. (Microphotograph.) Figs. 100—105. Transverse-sections through the Cerebellum of *Acipenser*. (Sketches.)

C, Cerebellum; c. g. m., the granular cell-mass of the Corpus cerebelli; E. th., ependymal thickening; F. rh. m., Fissura rhombo-mesencephalica; g. m., granular cell-mass; K, the median molecular ridge; L. e., Lobus externus; l. g. m., the granular cell-mass of the Lobus internus; L. i., Lobus internus; l. s. g. c., the lateral string of granular cells; M. l., molecular layer; m. s. g. c., the medial string of granular cells; Nc. i., Nuclei isthmi; P. m. a., Pars medialis auriculi; p. T. f., the posterior part of the Torus-formation; S. p., Sulcus paraauricularis; s. g. c., the granular cell-string of the Pars medialis; T. o., Tectum opticum; Vl. c., Valvula cerebelli; Z, the boundary-zone between Mes- and Metencephalon.

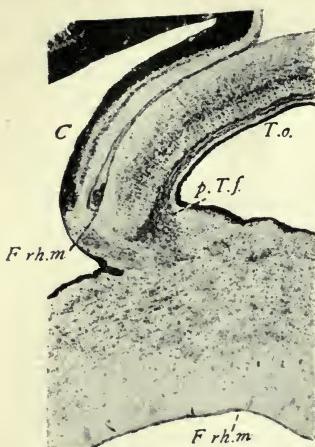


Fig. 98.

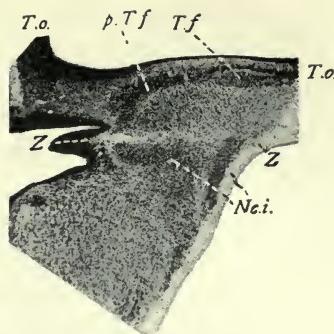


Fig. 99.



Fig. 100.

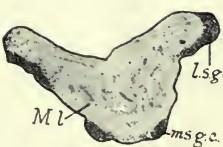


Fig. 101.

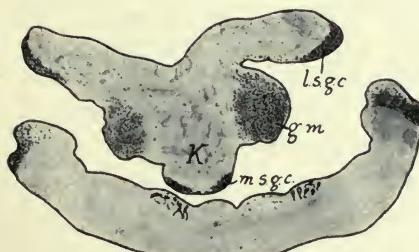


Fig. 102.

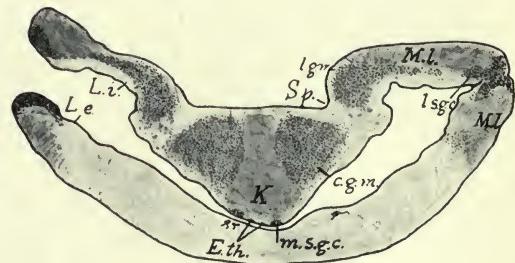


Fig. 103.

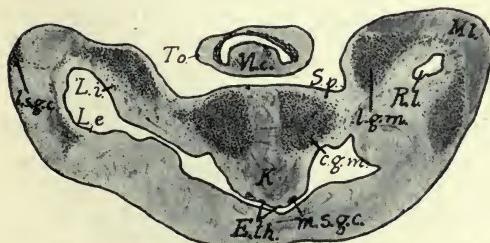


Fig. 104.

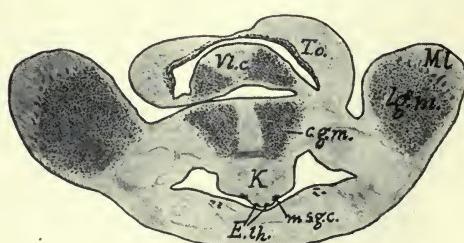


Fig. 105.

dorsal to them in *Acipenser*. This section of *Acanthias* (Fig. 106) ought clearly to be compared with section 101 in *Acipenser*, where to the left of Fig. 104 the fused granular cell-strings (l. s. g. c.) lie in the same position in relation to the molecular layer as in *Acanthias*.

It is further worthy of notice, that a number of larger cells are to be found in the lateral part of the Corpus, directly ventral to the line of connection with the Lobus internus, i. e. between the dorsal and ventral granular cell-agglomerations (these cells have also been described by JOHNSTON [1901], page 92).

Thus the granular cell-string of the Lobus externus in *Acipenser* as in *Acanthias*, bends over on to the Lobus internus, after which it passes away in a caudal direction. In Pars medialis the strings from the two sides unite, and can then be followed medially frontad into the Corpus<sup>1</sup>. The above described medial strings in *Acipenser* (m. s. g. c.), I assume to be homologous with the granular cell-ridges in *Acanthias*. These strings in *Acipenser* do not indeed appear to extend so far frontad as in *Acanthias*. Their exact position in regard to the decussation of the trochlear nerve I have not been able to determine, as this decussation is altogether untraceable on the haematoxilin-stained series which I have examined. Compared with the ridges in *Acanthias*, the strings in *Acipenser* give the impression of being rudimentary.

That the cells in these strings are true granular cells, appears evident from the fact: 1) that in the Pars medialis they pass continuously into the exactly similar strings in the Lobus internus, 2) that their size and appearance, so far as I have been able to judge, agree completely with the granular cells in the remaining parts of the Cerebellum. Medial to the strings are to be found two ependymal thickenings (E. th. Figs. 103—105). In *Acanthias* there are also to be found two distinct ependymal thickenings (E. th. Fig. 106) medial to the ridges. The granular cell-strings in *Acipenser* can therefore not be the medial ependymal thickenings, which occur in *Acanthias* and other fishes.

The bulk of granular cells in *Acipenser* should then correspond to the granular cells found scattered outside the ridges in *Acanthias* (EDINGER 1901).

With regard to the form of the Corpus cerebelli, I agree with JOHNSTON (1898), when he assumes that "the body and valvula have apparently been formed by a down-folding of the cerebellum in the middle-line, this folding has brought the molecular layer of the two folds into apposition and they

<sup>1</sup> In *Acanthias* the strings of granular cells do not, indeed, pass into one another in the Pars medialis auriculi as in *Acipenser*. When, however, the Cerebellum is primarily a paired structure (SCHAPER [1894]) and the corresponding cell-strings in *Salmo* at earlier stages are clearly also paired, it appears probably that the coalescence of the contra-lateral strings is secondary in *Acipenser* (and *Lepidosteus*).

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have fused to form the single median molecular layer" (page 591—592). If in other words, an imaginary medial groove, developed in that part of the Corpus which lies caudal to the decussation of Nervus IV, can be conceived as cutting down to the ependymal thickenings and then allowing it to develop and be magnified, it would be possible to get a type of cerebellum, which in form would correspond with the Cerebellum in Selachii, namely in *Acanthias*.

b) *Lepidosteus osseus*. I have examined a series of transverse-sections of *Lepidosteus osseus* (length 1,3 dm.) of which 105 sections at  $20\mu$  fall to the share of the Cerebellum. The fixation was not by any means perfect, but the tissue was well enough preserved to make an investigation of the topographical conditions of the various sections possible.

*Fig. 107, section 88.* A granular cell layer (s. g. c.) is here seen on the ventral side, which lies in the Pars medialis auriculi. Dorsally the section goes through the caudal part of the Corpus, the ventricle of which is seen in the figure. On both sides of the ventricle lies a mass of granular cells (g. m.), which dorsally and laterally is surrounded by a layer of Purkinje-cells and a molecular layer. A granular cellstring is lacking at the Crista cerebelli.

*Fig. 108, section 75* lies anterior to the Pars medialis. The Cerebellum-ventricle is in open communication with the 4<sup>th</sup> ventricle. Laterally (s. g. c.) lie strings of granular cells, which form a direct continuation frontad of the lateral parts of the above mentioned layer of granular cells (s. g. c. Fig. 107). The mass of granular cells in the Corpus begins dividing into two separate parts (c. g. m. and l. g. m.), a subdivision which is completed further frontad.

*Fig. 109, section 48.* On this are seen two dorsal grooves (S. p.), which divide a medial part: Corpus cerebelli, from two lateral parts: the Lobi interni. These grooves may therefore be termed Sulci paraauriculares. In the Lobus internus (L. i.) there lies ventrally a granular cell-string (s. g. c.), the one I have just mentioned. Laterally the Lobi is covered by a molecular layer (M. l.). Medial to this lies a granular cell-agglomeration (l. g. m.), which extends dorsally to the surface of the brain. A dorsally lying molecular layer reappears then in the Corpus. Under this and medially in the Corpus, lies another granular cell-agglomeration (c. g. m.), clearly distinguishable from the mass of granular cells, in the Lobus internus. Further caudad however, these granular cell-masses become fused (Figs. 108, 107). Between the principal masses of granular cells, we find a few scattered ones here and there in the Cerebellum. There exists also a number of larger cells (\* Fig. 109) between the masses of granular cells and ventral to the granular cell-mass in the Lobus internus, which I cannot by their appearance distinguish from the Purkinje-cells in the Purkinje-cell layer proper.

*Fig. 110, section 39* goes through the anterior part of the Corpus and the fusion-point of the Lobi interni and externi. On this point we see the frontal part of the granular cell-string in the Lobus internus (s. g. c.). The molecular layers (M. l.) in Lobi merge into one another. Between the molecular layer and Sulcus paraauricularis is found again the granular cell-mass (l. g. m.) in the Lobus internus. The granular cell-mass in the Corpus cerebelli (c. g. m.) is somewhat smaller frontad and continues into the Valvula cerebelli.

*Fig. 111, section 31*, is tangent to the anterior parts of the auricles. The granular cell-mass (l. g. m.) in this part is the frontal part of granular cell-mass in the Lobus internus. I cannot discover any ventral granular cell-mass in the Lobus externus under the Crista cerebelli.

The granular cell-strings in *Lepidosteus* are thus considerably reduced, are entirely missing medially in the Corpus, so far as I have been able to determine, as also in the Lobus externus. On the other hand, a caudo-medial part, connecting the granular cell-strings in the Lobi interni continues to exist. The remaining granular cells are disposed, as nearly as may be, in the same manner as in *Acipenser*. The granular cell-mass in the Lobus internus does not lie, it is true quite on the surface in *Acipenser*, the fibre substance which covers the same dorsally is however fairly thin and does not appear to be composed of typical molecular layer.

In regard to the form, especially of the Corpus cerebelli, the difference is greater. The medial ependymal thickenings lie near the surface dorsally and approximately in the same position as in *Acanthias*. Moreover, the whole of the Corpus cerebelli rises above the lobes, while in *Acipenser* it lies on a level with or lower than the lobes.

C. Teleostei (*Salmo salvelinus*, at stage E). Cerebellum in the Teleosts is usually subdivided into: 1) Valvula cerebelli, 2) Corpus cerebelli, 3) Auriculi cerebelli with Velum medullare posterius (Pars medialis auriculi). The embryonic development of the Valvula is treated below.

The boundary between the Corpus cerebelli and Pars auricularis is marked caudally by a well developed Sulcus postremus (Fig. 52).

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Fig. 106. Transverse section through the Cerebellum of *Acanthias* at stage 15,0 cm. (Sketch.) Figs. 107—111. Transverse-sections through the Cerebellum of *Lepidosteus*. (Sketches.) Figs. 112—116. Transverse-sections through the Cerebellum of *Salmo* at stage E. (Sketches.)

Ca. c., Canalis cerebelli; c. g. m., the granular cell-mass of the Corpus cerebelli; E. g., Eminentia granularis; E. th., ependymal thickenings; g. m., granular cell-mass; L. e., Lobus externus; l. g. m., the granular cell-mass of the Lobus internus; L. i., Lobus internus; M. l., molecular layer; P. c., Purkinje-cells; P. m. a., Pars medialis auriculi; R. l., Recessus lateralis; s. g. c., string of granular cells; S. p., Sulcus paraauricularis; S. po., Sulcus postremus; T. o., Tectum opticum; Vl. c., Valvula cerebelli.

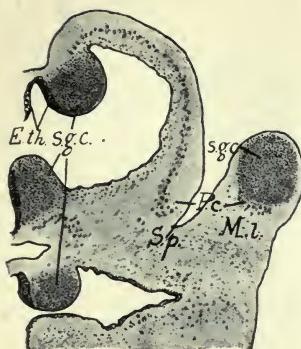


Fig. 106.

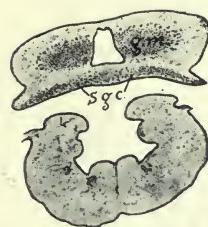


Fig. 107.

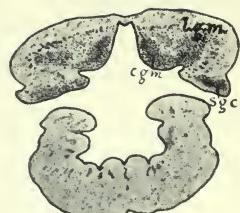


Fig. 108.

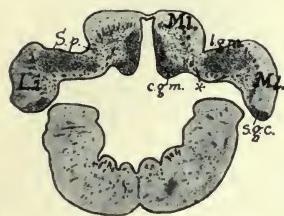


Fig. 109.

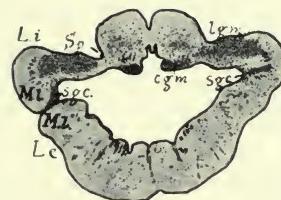


Fig. 110.

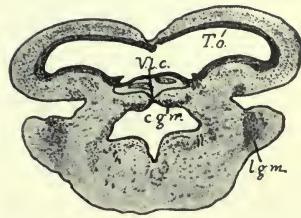


Fig. 111.

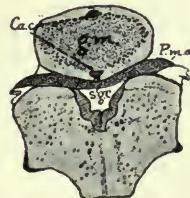


Fig. 112.

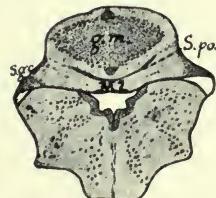


Fig. 113.

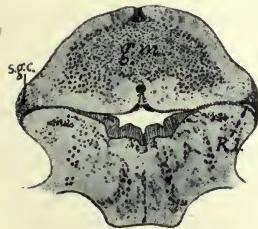


Fig. 114.

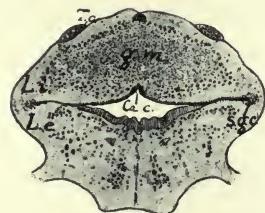


Fig. 115.

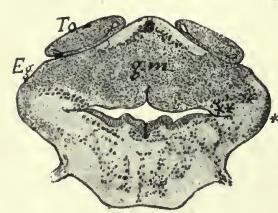


Fig. 116.

*Fig. 112.* This section goes through the caudal part of the Pars medialis which is composed of compactly disposed granular cells (s. g. c.). Dorsal to this part lies the dorsal portion of the Corpus, whose bulk consists of a granular cell-agglomeration (g. m.), surrounded by a Purkinje-cell- and molecular layer. *Canalis cerebelli* (SCHAPER [1894]) is transversely intersected dorsally and ventrally (Ca. c.).

The granular cell-string in the Pars medialis continues frontad in the Lobus internus: *Fig. 113.* This section goes through the anterior part of the Sulcus postremus (S. po.). Ventral to this groove lies a molecular layer (M. l.), which must thus be assigned to the Pars medialis. Dorsal to this groove lies the Corpus cerebelli. Granular cell-strings are lacking in the Crista cerebelli.

*Fig. 114.* The molecular layer in Pars medialis here bends over to pass into the ventral molecular layer in the caudal part of the Corpus. At this point, or immediately in front of the same, opens the ventro-caudal part of the *Canalis cerebelli* in ventricle IV. The granular cell-strings in the Lobus internus (s. g. c.) and the anterior part of the Recessi laterales (R. l.) can be observed laterally.

*Fig. 115.* This section lies somewhat frontad of the preceding one. The ventro-caudal part of the *Canalis cerebelli* (Ca. c.) is in open communication with the 4<sup>th</sup> ventricle. The Lobi interni and externi become merged laterally. On this point lies the anterior part of the granular cellstring (s. g. c.). Close to the intersected portions of the Tectum (T. o.), the granular cell-mass reaches the surface of the brain and divides a dorsal part of the molecular layer from a lateral. If the series of sections is followed frontad, it can be seen how this "naked" place widens more and more.

*Fig. 116.* On the right side of this section lies, lateral to the auricle, a granular cell-mass (\* *Fig. 116*), which somewhat further on (see the left side of the figure) passes into the lateral part of the bulk of granular cells (*Eminentia granularis* [E. g.]).

A comparison between *Salmo* and *Lepidosteus* can now be easily made. The boundary between the Corpus and the auricles should in *Salmo* clearly be drawn where the dorsal molecular layer in the Corpus finishes laterally. Between this layer and the corresponding layer in the auricles the granular cell-mass extends up to the surface as in *Lepidosteus*. It is not, indeed, possible to draw up any boundary in *Salmo* between the granular cell-mass in the Lobus internus and in Corpus, but this can easily be explained by the assumption that the scattered granular cells which are to be met with in *Lepidosteus* between the granular cell-agglomerations, have increased in number, so that a continuity has formed between them. Not till further frontad do the granular cell-masses in *Salmo* divide into two parts, of which one continues into the Valvula and the other covers the anterior part of

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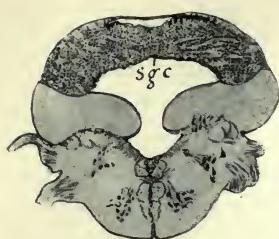


Fig. 117.

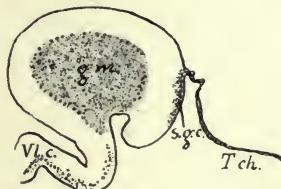


Fig. 118.

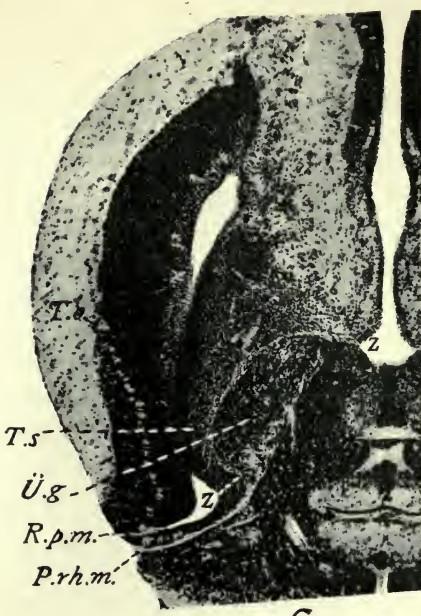


Fig. 119.

Fig. 117. Transverse section through the posterior part of the Cerebellum of *Osmerus*. (Sketch.) Fig. 118. Sagital section through the Cerebellum of *Osmerus*. (Sketch.) Fig. 119. Horizontal section of *Salmo* at stage D. (Microphotograph.)

C, Cerebellum; D. IV, Decussation of Nervus trochlearis; g. m., granular cell-mass; P. rh. m., Pllica rhombo-mesencephalica; R. p. m., Recessus posterior mesencephali; s. g. c., granular cell-string of the Pars medialis auriculi; T. ch., Tela chorioidea; T. o., Tectum opticum; T. s., Torus semicircularis; Ü. g., "Übergangsganglion"; Vl. c., Valvula cerebelli; Z, the boundary-zone between the Mes- and Metencephalon.

the auricles. I am unable to determine in what measure the lateral granular cells in the auricles, visible to the right on Fig. 116 \*, correspond with the ventral granular cell-mass in the Lobus externus of *Acipenser*.

In *Salmo* a molecular layer projects into the Corpus in a medial direction from the molecular layer in the auricles \*\* Fig. 116. This layer is connected caudally with the molecular layers in Pars medialis and with the ventro-caudal part of the Corpus. The corresponding Purkinje-cell layer lies in the same position as the large cells, described above in *Lepidosteus*, and also by JOHNSTON (1901) in *Acipenser*. It may be assumed that these cells, which at least in *Lepidosteus*, greatly resemble the true Purkinje-cells in *Salmo*, have been regularly arranged and form together with cell-neurites, a typical molecular layer. The granular cell-strings in the Pars auricularis are in complete conformity to the corresponding strings in *Lepidosteus*.

Thus the Cerebellum in *Salmo* differs from the Cerebellum in *Lepidosteus*, chiefly by the considerable increase in the number of granular cells. This

must also be the cause of the Cerebellum-ventricle growing together to a canal-rudiment: the Canalis cerebelli.

Before passing on to a description of the Valvula cerebelli, it seems suitable to say a few words about the Cerebellum in fully developed bony fishes. I have examined *Osmerus eperlanus* and *Labrus rupestris*.

Caudally in the Cerebellum in *Osmerus* lies a granular cell-agglomeration (s. g. c. Figs 117, 118), which clearly is the granular cell-string in Pars medialis auriculi described in *Salmo*. In *Osmerus*, Sulcus postremus has disappeared, and Pars medialis become merged in the Corpus. It is further characteristic for this species, that the whole length of the Lobus internus is united with the Lobus externus. The granular cell-string in the Pars medialis can be traced frontad as two lateral strands close to the ventricle. The granular cell-mass in the Lobus internus is powerfully developed and forms two eminences, one on each side of the brain (Eminentia granularis). In other respects *Osmerus* corresponds with *Salmo*.

A well-defined granular cell-string is lacking in the Pars medialis in the higher bony fishes, as e. g., in *Labrus*. On the other hand, the strings in the Lobi interni are to be found lying in the same position as in *Osmerus*. In the Pars medialis these strings turn into a small number of scattered granular cells, which form the remaining part of the granular cell-string in this part. The Eminentia granularis are not so powerfully developed as in *Osmerus*. Corpus cerebelli is however considerably larger in *Labrus*. The caudal part of the Corpus projects a good deal over the Pars medialis.

*Valvula cerebelli*. Already at stages 0,7 and 0,8 cm. in *Salmo*, it is possible, on haemalum-stained sagital-sections of the brain, to discern the decussation of the trochlear nerve as a lighter spot in the embryonic cell-mass (D. IV Fig. 41). At these stages the decussation lies fairly close to the Fissura rhombo-mesencephalica and thus in a position normal in the rest of the vertebrates. It is possible to observe during the process of development, how the decussation becomes more and more displaced in a caudal and ventral direction, so that it finally, in the fully developed brain, lies right under the valvula. As at earlier stages, Fissura rhombo-mesencephalica lies where the thin caudal wall of the Mesencephalon passes into the Valvula cerebelli, the boundary between the Mes- and Metencephalon should at later stages also be drawn at this point. The displacement of the trochlearis-decussation can therefore only be explained by the growth or expansion of the part between the boundary-plane and the decussation. Although this part takes the shape of a fold, under the Tectum, it is not thereby proved that it (the oriment of the Valvula) increases frontad. There is also a possibility of the caudal part of the Tectum growing caudad. As a matter of fact, this latter seems to be the case, at any rate in the beginning. If the position of the anterior part of the Valvula fold is compared in relation

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to the Sulcus intraencephalicus posterior viz. the boundary-line, it becomes apparent that no change has taken place in this position although the Valvula has enlarged and developed more and more. It is not till the eldest stages (D. [Fig. 52]) that a portion of the Valvula (that in front of "Übergangsganglion" of MAYSER) lies in front of the boundary-plane, and has thus grown in a frontal direction in relation to the latter.

With the development of the Valvula cerebelli, the boundary-plane between the Mes- and Metencephalon becomes more and more curved. On horizontal sections (Fig. 119) the boundary-line (Z—Z) forms curves with the convexity pointing frontad. These distinct lines form the anterior boundary to the Isthmus region.

Immediately behind the boundary-line lies a compact mass of cells, which forms the so-called "Übergangsganglion", which thus lies in the Metencephalon.

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